The High Risk of Extinction for the Natural Fall-Run Chinook Salmon Population in the
Lower Tuolumne River due to Insufficient Instream Flow Releases

Carl Mesick, Ph.D.
Energy and Instream Flow Branch
U.S. Fish and Wildlife Service
2800 Cottage Way, Suite W-2605
Sacramento, California 95825
4 September 2009

ABSTRACT

Fall-run Chinook salmon (*Oncorhynchus tshawytscha)* escapement in the Tuolumne
River, Central Valley of California, has declined from 130,000 salmon during the 1940s
to less than 500 salmon during the early 1990s and in 2007. The Tuolumne River's
naturally produced fall-run Chinook salmon population was judged to be at a high risk of
extinction since 1990 because escapement has repeatedly declined to low levels, the
population has declined rapidly, and the mean percentage of hatchery fish in the
escapement has been high. A potential consequence of the population declining to 157
salmon from 1990 to 1992 and the resulting loss of genetic viability is that the
population's productivity declined by about 50% from 1996 to 2005.

The decline in escapement is primarily due to inadequate minimum instream flow
releases from La Grange Dam in late winter and spring during the non-flood years. In
most years, except spring 2005, the number of smolts migrating from the Tuolumne
River has been a good predictor of adult recruitment. The estimated number of smolt-
sized outmigrants passing rotary screw traps near the mouth of the Tuolumne River
approximately doubled in response to 2- to 3-day, 3,000 cfs pulse flows in late winter that
inundated about 500 acres of floodplain habitat. Adult recruitment more than doubled
when prolonged late winter pulse flows of at least 3,000 cfs occurred and the water
temperatures near the river's mouth were kept below 15°C through at least early May.
Another problem is that up to 58% of Merced River Hatchery Chinook salmon strayed to
the Sacramento River Basin whenever flows in the San Joaquin River were less than
3,500 cfs for 10 days in late October. Other analyses show that spawner abundance,
spawning habitat degradation, and the harvest of adult salmon in the ocean have not
caused the decline in escapement.

INTRODUCTION

The escapement of fall-run Chinook salmon (*Oncorhynchus tshawytscha)* population in the Tuolumne River, which is a tributary to the San Joaquin River in the Central Valley of California, has gradually declined from 130,000 salmon during the 1940s to less than 500 salmon during the early 1990s and in 2007 (Fig. 1). Since the 1940s, escapement has been correlated with the mean flow at Modesto (U.S. Geological Survey gauge 1129000) from 1 February through 15 June two years before escapement when the Age 3 salmon were rearing and migrating as juveniles toward the ocean. This correlation suggests that escapement has been primarily determined by the rate of juvenile survival, which is primarily determined by the magnitude and duration of late winter and spring flows since the 1940s.
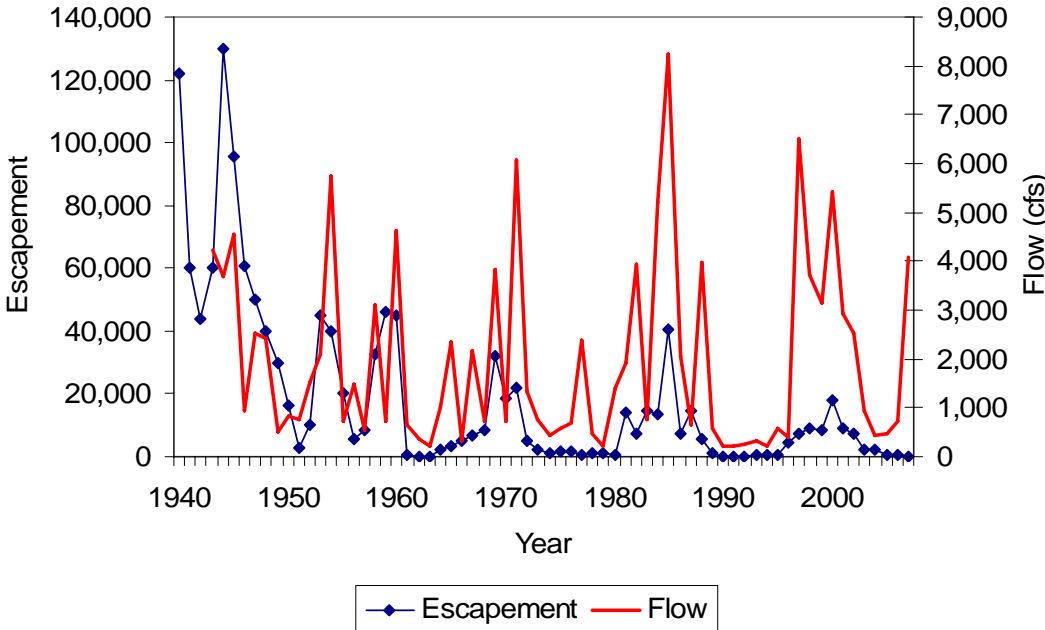

Fig. 1. Tuolumne River fall-run Chinook salmon escapement and mean streamflow in the Tuolumne River at Modesto (DWR gauge data for MOD) from 1 February to 15 March two years prior to the escapement estimate from 1940 to 2007. Escapement estimates from 1952 to 2007 are published in the California Department of Fish and Game GrandTab file available at www.CalFish.org and those from 1940 to 1951 are cited in Fry (1961).

I present evidence below that the decline in escapement is primarily due to the inadequate minimum instream flow releases from La Grange Dam (river kilometer 84.0) during the non flood years. Since the 1940s, escapements have declined to low levels during extended droughts whereas extended flood control releases of at least 3,000 cfs occur during the winter and spring period approximately 30% of the years (Figure 1). The enlargement of Don Pedro Reservoir in 1971 from 290,000 acre-feet to 2,030,000 acre-

feet (TIM and MID 2005) reduced the frequency of prolonged late winter and spring flood control releases by a small degree from 28% of the years prior to 1971 to 24% of the years since 1971, because the reservoir is kept full to maximize the certainty of the water supply. The minimum flow requirements under the original Federal Energy Regulatory Commission (FERC) License (Article 37) ranged between 40,123 acre-feet per year in the driest years to 123,210 AF per water year in wet years from 1971 to 1995 (TID and MID 2005), which is about 14% of the unimpaired flows in the Tuolumne River. In 1996, Article 37 was amended and the minimum flow requirements increased to a range of 94,000 acre-feet in the driest years to 300,923 acre-feet during the wet years (TID and MID 2005), which is about 33% of the unimpaired flows. Additional flows were released during the relatively dry years since 1996 during April and May on a temporary basis to study the effects of flow and Delta exports on the survival of tagged juvenile fall-run Chinook salmon released in the lower San Joaquin River near Stockton (SJRGA 2007). I provide evidence below that the Tuolumne River salmon population of naturally produced fish is at a high risk of extinction since 1996 due to the inadequate instream flow releases during the relatively dry water years as required under Article 37.

My risk of extinction analyses are based on the criteria developed by Lindley et al. (2007), who characterized the risk of extinction for Chinook salmon populations in the Sacramento-San Joaquin Basin relative to population size, rates of population decline, catastrophes, and hatchery influence. To estimate the number of naturally produced fall-run Chinook salmon in the lower Tuolumne River from 1981 to 2007, I rely on two analyses. The first analysis, which is described in Mesick et al. (2009a), estimates the rates that hatchery produced Chinook salmon with coded-wire-tags (CWTs) and those that were untagged but released in association with the CWT releases were recovered in the lower Tuolumne River from 1981 to 2007. This period was selected because of the availability of CWT recovery data needed to estimate the number of hatchery fish in the escapement (Mesick et al. 2009a). The second analysis, which is described here, assumes that the untagged Central Valley hatchery produced Chinook salmon that were released during the same month and in the same general location (e.g., tributary, mainstem Sacramento or San Joaquin rivers, or Bay-Delta releases) would return to the Tuolumne River at the same rate as the CWT salmon released during the same month and general location. Finally, I show the relationships between the smolt-sized (>70 mm Fork Length) Chinook salmon that outmigrated from the Tuolumne River, the number of naturally produced adult recruits that survive to Age 2, and the instream flow releases into the lower Tuolumne River from LaGrange Dam to provide evidence that the Chinook salmon population is at risk of extinction due to inadequate instream flow releases.

Lindley et al. (2007) characterized Chinook salmon populations with a high risk of extinction (greater than 20 percent chance of extinction within 20 years) as those with a total escapement that is less than 250 spawners in three consecutive years (mean of 83 fish per year), a precipitous decline in escapement, a catastrophe defined as an order of magnitude decline within one generation occurring within the last 10 years, and a high hatchery influence. Populations with a low risk of extinction (less than 5 percent chance of extinction in 100 years) have a minimum total escapement of 2,500 spawners in three

consecutive years (mean of 833 fish per year), no apparent decline in escapement, no catastrophic declines occurring within the last 10 years, and a low hatchery influence. Populations with a moderate risk of extinction are those at intermediate levels to the low and high risk criteria (e.g., total escapement in three consecutive years between 250 and 2,500 spawners. The overall risk for the population is determined by the criterion indicating the highest risk of extinction. These criteria are slight modifications of those used by Allendorf et al. (1997).

METHODS

The methods used to estimate the number of naturally produced adult recruits that survived to Age 2 are described in Mesick et al. (2009b). Described below are the methods used to (1) estimate the number of untagged hatchery produced Chinook salmon releases that returned to the lower Tuolumne River in the adult escapement; (2) estimate the number of smolt-sized Chinook salmon that outmigrated from the Tuolumne River based on rotary screw trap studies, and (3) adjust the estimated number of naturally produced adult recruits to account for fish that strayed to the Sacramento River Basin.

Untagged Hatchery Salmon Estimates

The estimated numbers of unmarked hatchery fish that returned to the Tuolumne River as adult salmon are based on the assumption that the unmarked hatchery fish would have returned to the Tuolumne River at the same rates that the marked hatchery fish returned to the Tuolumne River if they were released during the same month and in the same general location. The number of unmarked fish released from each hatchery was obtained from the CDFG annual reports for the Feather River, Nimbus, Mokelumne River, and Merced River hatcheries. Some of the Merced hatchery release data was obtained from planting release records.

Most of the CWTs recovered as adults in the Tuolumne River (Table 1) were released as juvenile salmon that were produced at the Merced River Hatchery (MRH), Mokelumne River Fish Installation (MRFI), Nimbus Fish Hatchery (NFH), and the Feather River Hatchery (FRH) as described in Mesick et al. (2009). Relative to the number of juveniles released, the highest adult recovery rates in the Tuolumne River escapement occurred for juveniles released in the Delta and Bay and moderate recovery rates occurred for juveniles released in the Sacramento and San Joaquin rivers (Table 1). I define the Delta and Bay region of the Central Valley as the areas where the flow from the Sacramento and San Joaquin rivers mix: downstream from Collinsville on the Sacramento River, New Hope Landing on the Mokelumne River, and Jersey Point on the San Joaquin River. Straying rates of hatchery fish, and thereby recovery of hatchery fish in the Tuolumne River, tend to increase the further that the juvenile salmon are trucked and released downstream toward the Delta and Bay where their natal waters are mixed with flows from other rivers (Mesick et al 2009a).

There were few adults recovered in the Tuolumne River from juvenile releases in the other Central Valley tributaries with the exception of MRH releases in the Merced River (Table 1). Therefore, I assumed that none of the untagged salmon from the FRH, NFH, and MRFI that were released in the other Central Valley tributaries were recovered in the Tuolumne River.

Another factor affecting the recovery rates of hatchery adults in the Tuolumne River was the timing of the juvenile releases. The highest recovery rates occurred from yearling releases in October and November and smolt releases in April and May, and low rates occurred during the other months (Mesick et al. 2009a). The highest recovery rates occurred from yearling releases in October and November for a few comparisons that could be made within the same year, whereas they were many more smolt releases over a variety of water year types and the mean recovery rates occurred for the smolt releases based on the entire dataset (Table 1).

For about half the releases of untagged hatchery juveniles there were releases of CWT juveniles during the same year, month, and general location that I used to estimate the number of untagged recoveries in the Tuolumne River. In these cases, I used the mean monthly-, age-specific CWT recovery rates to estimate the number of untagged salmon in the Tuolumne River escapement when the tagged and untagged fish were released during the same year, month, and general location (tributary, mainstem river, or Bay-Delta). For example, if 0.0033% of the FRH fish with CWTs released in the Bay-Delta in June 1985 returned to spawn in the Tuolumne River as Age 3 salmon in fall 1987, then I assumed that 0.0033% of the untagged FRH salmon released in the Bay-Delta in June 1985 returned to spawn in the Tuolumne River as Age 3 salmon in fall 1987.

There were many instances when no paired releases of tagged and untagged fish were made in the same month and a few cases when there were no CWT releases in the same year. I believe that there are two main factors that affected the number of unmarked hatchery strays that returned to the Tuolumne River: (1) the survival of the planted juveniles, which primarily was affected by the month and location of planting, and (2) the relative amount of flow from the Tuolumne River relative to the San Joaquin River when the adults were returning. Another obvious pattern in the annual variation was that few if any out-of-basin CWTs were recovered in the Tuolumne River from juvenile releases made during the 1987 to 1992 drought when instream flow releases were low (Table 1) and during spring 2005 and 2006, when ocean conditions were unfavorable (Lindley et al. 2009).

I employed a simple empirical approach to estimate recovery rates for the untagged hatchery releases when there were no paired CWT release data. For those cases when there were recovery estimates for at least one month in a year, but not all months when untagged releases were made from the same hatchery and at the same location, I computed the recovery rate for the months without specific CWT data by multiplying the known CWT recovery rate by the ratio of the mean of all years for Age 3 salmon during the month without CWT data divided by the mean for all years for Age 3 salmon during the month with the CWT data. For example in April 1995, CWT FRH juveniles were

released in the Delta, but there no CWT Delta releases in May. The recovery rate for Age 2 fish in the Tuolumne from this cohort released in April is 0.00858%. The mean recovery rate of Age 3 fish for April and May releases is 0.0013% and 0.0005%, respectively for the FRH releases in the Delta. The computed recovery rate for Age 2 fish for the May FRH releases is 0.00330% (0.00858% * 5/13).

For the few cases when there were no corresponding CWT releases in the same year, I used three sets of CWT recovery estimates. For the 1987 to 1992 drought years, I used the mean age-specific CWT recovery rates for the drought years (Table 1). For spring 2005 and 2006, I used the mean age-specific CWT recovery rates during spring 2005 and 2006, which were zero, to estimate the recoveries of all unmarked fish released during 2005 and 2006. For all the other years, I used the mean age-specific recovery rates for all years (Table 1).

One particular problem was that there were very few releases of NFH CWT fish that could be used to estimate the recoveries of unmarked NFH fish in the Tuolumne River. Therefore, I assumed that the NFH fish that were planted in the Bay-Delta and Sacramento River would stray to the Tuolumne River at the same rate as the FRH fish as both hatcheries are in the Sacramento River Basin and therefore their fish should have similar homing tendencies. This seems reasonable based on the few available comparisons between the two sets of recovery estimates. For example, the mean recovery rate of Age 3 fish from the FRH releases in the Bay-Delta in May was 0.0005% whereas it was 0.0007% for NFH releases in the Bay-Delta in May (Table 1).

Few CWTs from the Coleman National Fish Hatchery were recovered in the Tuolumne River regardless of where they were planted in the Bay-Delta, Sacramento River, or Battle Creek or when they were planted (Mesick et al. 2009). However, the lack of CNFH recoveries in the Tuolumne River may be an artifact that few CNFH CWTs were released in April and May in the Bay-Delta and Sacramento River during non-drought years when Tuolumne River recoveries would have been expected. A total of 334,359 CNFH CWTs were released in April and May in the Bay-Delta CWTs (1982 to 1986 only) and a total of 610,313 CNFH CWTs were released in the Sacramento River (1981 to 1984 only) during non-drought years (Mesick et al 2009a) and these numbers are quite low compared to the other hatcheries (Table 1). Most CNFH CWT releases in the Bay-Delta and Sacramento River were made in February and March, when survival rates were generally low for pre-smolt juveniles. Nevertheless, in keeping with an empirical approach, it was assumed that no untagged CNFH salmon returned to the Tuolumne River.

There are several sources of potential error associated with my estimates of untagged hatchery fish in the escapement and my estimates should be considered as an index that reflects trends over time. The estimates of hatchery fish with CWTs are relatively accurate for the Tuolumne River, particularly since 1983 when the recovery data were accurately recorded and many carcasses were examined for CWTs (Mesick et al 2009a). Most of the uncertainty associated with the CWT estimates is that some of the juveniles releases were so small that no adults were recovered during the Tuolumne River

escapement surveys. It is impossible to determine the true recovery rates in those cases and it is difficult to know the minimum number of juveniles that needed to be released each year to provide accurate results. I believe that my estimates of untagged hatchery fish based on paired releases with CWT fish in the same general location, month, and year are reasonably accurate but there they have a much higher degree of uncertainty because small differences in timing (e.g., early May versus late May juvenile releases) and location (Central Delta versus North Delta releases) can affect the return rates to the Tuolumne River. There are other estimates for which I use CWT rates from different months, years, and/or hatcheries that have high levels of uncertainty. It is highly likely that a complex statistical analysis would show that 95% confidence intervals would be very large compared to the mean values. Nevertheless as I discuss in the Results section, using my estimates of untagged hatchery fish do not change any of my conclusions because my estimates of untagged hatchery fish are near zero when escapements are low (i.e., no effect to minimum population size) and they are rarely a substantial percentage of the high escapements (i.e., little effect on population trends and percentages of hatchery fish).

<center>Smolt-Sized Outmigrant Estimates</center>

One EG Solutions, Inc. rotary screw trap (2.4 m diameter) was fished at Shiloh (river kilometer 5.5) in 1998 whereas two traps were fished side by side at the Grayson site (river kilometer 8.4) from 1999 to 2008 during the majority of the smolt outmigration period from April 1 to at least until May 29 (Palmer and Sonke 2008). In spring 2008, a weir was constructed about 15 meters upstream of the trap to divert more flow and juvenile salmon into the trap (Palmer and Sonke 2008). The California Department of Fish and Game provided the catch data for all years sampled.

Trap capture efficiency tests were conducted in most years by typically marking about 2,000 hatchery juveniles (500 to 3,000) with dye and releasing them at about dusk about 0.4 kilometers upstream of the traps from 1999 to 2004 (Fuller 2005) and about 1.6 kilometers upstream of the trap in 2006 and 2008 (Palmer and Sonke 2008). The tests were repeated over a range of flows and the percentage of the marked fish that were captured in the traps was computed for each release group. The number of efficiency tests with smolt-sized fish conducted each year was 8 tests at Shiloh in 1998 and ranged between 0 to 12 (mean 5.4) tests at the Grayson site from 1999 to 2008 (Palmer and Sonke 2008). The calibration tests conducted in a given year did not always represent the entire flow range that occurred in a given year and there were few if any replicate tests at the same flow. Almost all of the Grayson trap tests had been conducted at flows $\leq$ 1,500 cfs; whereas there were 3 tests at about 2,000 cfs, 3 tests at about 3,000 cfs, and five tests in 2006 at flows ranging between 4,764 and 7,942 cfs. These flow data were measured at the U.S. Geological Survey gauge 1129000 at Modesto. Another problem is that there was an inadequate number of recaptures from the eight tests in 1998 (mean 2.4 recaptures per test) and five tests in 2006 (mean 2.6 recaptures per test). The CVPIA Comprehensive Assessment and Monitoring Protocol for rotary screw trap studies recommends that a minimum of 20 fish should be recaptured during each test (Anonymous 1997).

I developed efficiency models that I used to estimate the abundance of smolt-sized fish ($\geq$ 70 mm fork length) for the Shiloh trap with the 1998 data (Fig. 2) and for the Grayson traps with the combined 1998 to 2001, 2003, 2004, and 2006 data (Fig. 3) using multiple linear regressions. The results of the trap efficiency tests for spring 2002 were not used to generate the model of smolt-sized fish for the Grayson trap, because the efficiencies were abnormally low compared to all the other years, which suggests a temporary abnormality in the test procedure. I did not use the spring 2008 efficiency data because the weir used to improve capture efficiencies in 2008 was not used in previous years. The percentage of marked fish recaptured was regressed against the natural log (Ln) of flow at Modesto and the mean fork length (FL) of the release group. I conducted a second regression model to generate adjusted-R^2 and probably values by transforming the efficiency percentages into their natural logs. However, these values do not fully reflect the high level of uncertainty for smolt abundance estimates at flows greater than about 3,000 cfs (spring 1998, 2005, and 2006 estimates) due to the relatively low number of tests, the low number of recaptures per test, and the low efficiencies. For example, although the recovery rates at the 2006 high flows were relatively consistent ranging between 0 and 0.42% (mean 0.21%), a potential error of 0.1% could result in a 50% change in the estimated smolt abundance. The calibration models are as follows:

Shiloh Trap Efficiency Model, 1998

% Juveniles Captured = -0.00106*LN (Modesto Flow cfs))-(0.00008773*FL) + 0.01733; low efficiency values were truncated at 0.0005. The adj-R^2 for this model for natural log transformed efficiency estimates is 0.33 and $P = 0.1602$.

Grayson Trap Efficiency Model For Smolts, 1999-2007

% Juveniles $\geq$ 70 mm FL Captured = -0.02190*LN (Modesto Flow cfs)) - (0.0004120*FL) + 0.22453; low efficiency values were truncated at 0.002. The adj-R^2 for this model for natural log transformed efficiency estimates is 0.35 and $P = 0.0000$.

Adjustments For Sampling Periods

Three adjustments were made to the juvenile abundance estimates. The 1998 estimates were multiplied by 7/5 because weekends were not sampled. The traps were operated 7 days a week during all the other years. Two other adjustments were necessary because rotary screw trapping did not span the entire smolt outmigration period, which typically is March 20 to June 15 based on years when the Grayson and Shiloh rotary screw trap studies encompassed the entire period. Sampling did not begin until early April during 2003 to 2005 whereas sampling ceased in late May or early June in most other years. I standardized the periods for all studies to March 20 to June 15 by assuming that the abundance estimates per day for the unsampled days would have been the same as the estimated mean abundance per day at the beginning or the end of the sampling period. For 2003 to 2005, when sampling began on April 1 or 2, I multiplied the mean abundance estimate per day for each day sampled through April 10 times the number of unsampled
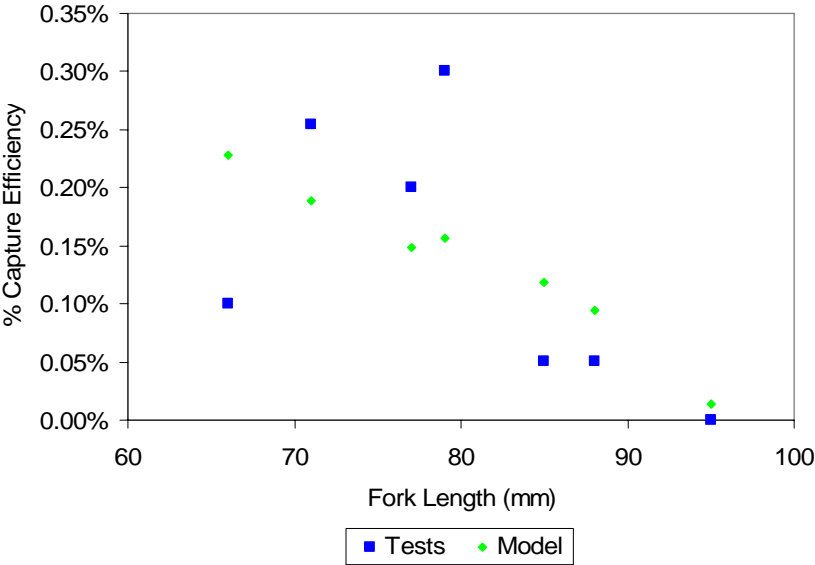
Fig. 2. Trap capture efficiency estimates (Tests) based on the percentage of marked releases of smolt-sized fish that were captured in the single rotary screw trap at Shiloh in the Tuolumne River (rkm 5.5) in spring 1998 relative to their mean fork length of all fish released and efficiency model predictions (Model) based on a multiple regression model of the capture efficiencies relative to the natural log of Modesto flows and the mean fork length of the juvenile salmon at release.

Fig. 3. Trap capture efficiency estimates (Tests) based on the percentage of marked releases of smolt-sized fish (> 65 mm fork length) that were captured in the paired rotary screw traps at Grayson in the Tuolumne River (rkm 8.4) during 1999-2001 and 2003-2005 relative to the mean streamflow at Modesto and efficiency model predictions (Model) based on a multiple regression model of the capture efficiencies relative to the natural log of Modesto flows and the mean 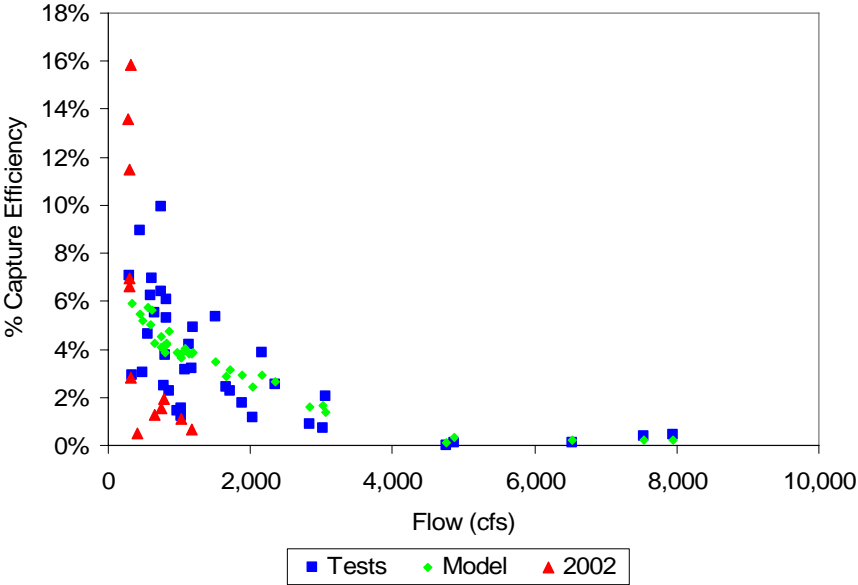fork length of the juvenile salmon at release. The 2002 estimates were omitted from the model because they were abnormally low compared to all other years.

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days from March 20. For the other years when sampling ceased before June 15, I multiplied the mean abundance estimates per day for each day sampled for the last few days when catch rates were relatively consistent times the number of unsampled days. Table 2 presents the data used to compute these adjustments.

Recruitment Estimates Adjusted For Straying

I estimate the percentage of the adult MRH fall-run Chinook salmon with CWTs that were recovered in the Sacramento River Basin relative to the total number recovered in all Central Valley river during the fall-run Chinook salmon escapement surveys from 1979 to 2007 (Mesick et al. 2009a). The estimated stray rates are presented in Table 3.

The analyses of risk assessment are based on the number of spawners in the escapement. However, assessments of the effects of instream flow and other environmental factors on the Tuolumne River escapement are best made with estimates of either juvenile production or adult recruitment that are not affected by ocean harvest, which varies substantially over time (see Results). To focus my assessments on the effects of late winter and spring flows on juvenile survival and not include the effects of fall pulse flows on adult straying, I adjusted my recruitment estimates to compensate for the number that strayed to the Sacramento River Basin when fall pulse flows were inadequate. This adjustment had substantial effects on the recruitment estimates in some years as the estimated straying rates varied from near zero to up to 58% (see Results).

I adjusted the recruitment estimates to reflect normal stray rates that are no higher than 6% annually should adequate fall pulse flow releases occur every year. I made these adjustments by computing the difference between the observed CWT stray rate (Table 3) and a 6% stray rate and then multiplying the difference plus 1 times the escapement to compute a low-stray adjusted escapement estimate (Table 3). I computed a low-stray adjusted recruitment estimate (Table 3) using the low-stray adjusted escapement estimates according to the methods described in Mesick et al. (2009b).

RESULTS

The results are presented in two sections. The first pertains to the risk of extinction analysis. The second pertains to an analysis of the environmental factors that control salmon recruitment for the Tuolumne River.

Risk Of Extinction Analysis

The Tuolumne River fall-run Chinook salmon population is at a high risk of extinction based on the criteria by Lindley et al. (2007) because the total escapement of naturally produced fish was estimated to be 1,232 spawners from 2006 to 2008 (i.e., moderate risk), there was a precipitous decline in escapement (i.e., high risk), there was a catastrophic decline in escapement over a generation between 2000 and 2006 (i.e., high

risk), and the mean percentage of hatchery fish in the escapement was 19.2% since 1998 (i.e., high risk). The overall risk for the population is determined by the criterion indicating the highest risk of extinction (Lindley, Fishery Biologist, National Marine Fisheries Service, personal communication). My analyses are based on estimates of the number of naturally produced and hatchery produced adult fall-run Chinook salmon that have returned to the Tuolumne River between 1981 and 2007 (Table 4).

Effective Population Size

The effective population size criteria relates to the loss of genetic diversity (Lindley et al. 2007). The effective population consists of individuals that are reproductively successful, including grilse (Allendorf et al. 1997). In Chinook salmon populations, not all individuals are reproductively successful and the mean ratio of the effective population size to total escapement over a three year period (N_e/N) has been estimated to be 0.20 based on spawner-recruit evaluations of over 100 salmon populations from California to British Columbia (Waples et al. 2004 as cited in Lindley et al. 2007). A few examples of why adult salmon may not reproduce successfully in the Tuolumne River include: (1) redd superimposition that destroys eggs; (2) spawning in habitats with excessive levels of fines; and (3) low survival rates for juveniles that migrate late when high water temperatures in the lower Tuolumne River are unsuitable for survival. Therefore based on effective population size (Ne), the Tuolumne River could be considered to be at high risk if annual escapement (N) drops below a mean of 83 fish for three consecutive years and at low risk if escapement remains above a mean of 833 fish for three consecutive years.

Since the Federal Energy Regulatory Commission license for the Don Pedro Project was amended in 1996 to improve minimum instream flows in the lower Tuolumne River and the minimum flow allocation was 94,000 acre-feet per water year, the number of naturally produced Chinook salmon in the escapement declined to a low of 1,409 between 2005 and 2007 (Table 4). A total of 1,409 salmon is within the range of 250 to 2,500 for the moderate risk of extinction criterion of Lindley et al. (2007). If one assumes that there were no untagged hatchery salmon in the 2008 escapement, then the total declines to 1,232 for the 2006 to 2008 period (Table 4). This total would be lower than 1,232 if there were untagged hatchery salmon in the 2008 escapement. Furthermore, it is highly likely that the number of naturally produced adults that return in the Tuolumne River escapement will continue to decline in fall 2009, because the estimate of smolt-sized Chinook salmon that outmigrated from the Tuolumne River was unusually low in spring 2007 and 2008, 937 and 2,351 respectively (Palmer and Sonke 2008), which is a small fraction of the 351,943 and 97,424 smolt outmigrants in 2005 and 2006, respectively, that produced the 2007 and 2008 escapements.

Prior to the 1996 improvement in minimum instream flow requirements, when the minimum flow allocation was 40,123 acre-feet per water year, the natural escapement dropped to a low of 157 adult salmon between 1990 and 1992 (Table 4). Allendorf et al. (1977) concluded that the Tuolumne River fall-run Chinook salmon population was at a high risk of extinction prior to 1996 based on the effective population size and population

decline criteria described by Lindley et al. (1997). However, the 1996 minimum instream flow requirements increased the minimum Tuolumne River fall-run Chinook salmon escapements from a level indicating high risk to a level indicating a moderate risk of extinction based on Lindley et al.'s (2007) population size criterion alone.

Population Decline

Another serious threat to the viability of natural salmonid populations identified by Lindley et al. (2007) is a precipitous decline in escapement, which has occurred on the Tuolumne River. Lindley et al. (2007) define a precipitous decline as a decline within the last two generations (6 years) to an annual run size of 500 spawners or fewer or a run size greater than 500 spawners but declining at a rate of at least 10% per year. Lindley et al. (2007) recommend that the population decline rate should be computed as the slope of the log of the escapement versus time multiplied by 100 over a ten year period.

The escapement of natural spawners in the Tuolumne River meets both of these criteria. First, the natural escapement declined to fewer than 500 spawners in fall 2007 and 2008 (Table 4). Second, the population declined at an average rate of 19.2% per year from 1999 to 2008 (Fig. 4).
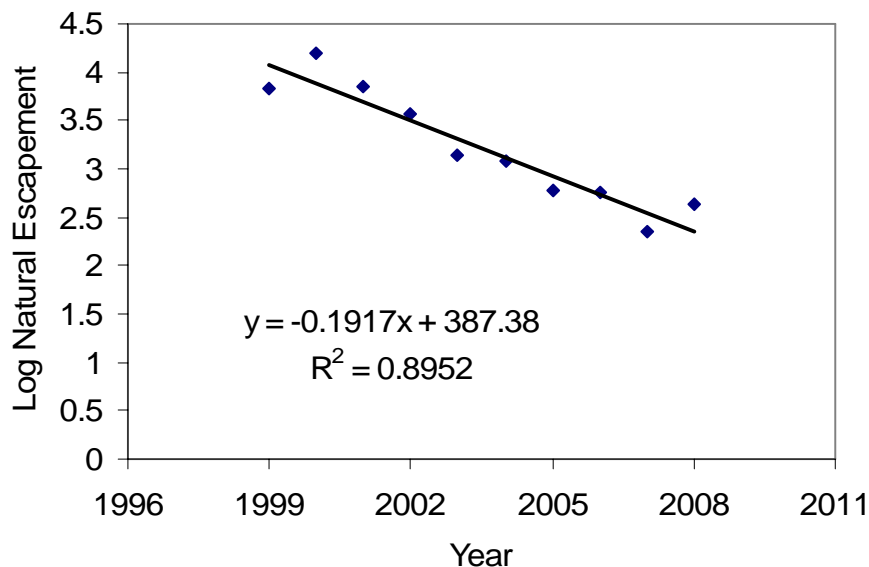
Fig. 4. The log of the natural escapement of fall-run Chinook salmon in the Tuolumne River from 1999 to 2008. The slope of the regression indicates that the population decline was 19.2% per year.

Catastrophe

Catastrophes are defined by Lindley et al. (2007) as instantaneous declines in population size due to events that occur randomly in time that reflect a sudden shift from a low risk state to a higher one. They view catastrophes as singular events with an identifiable

cause and only negative immediate consequences, as opposed to normal environmental variation which can produce very good as well as very bad conditions. Some examples of catastrophes include disease outbreaks, toxic spills, or volcanic eruptions. A high risk situation is created by an order of magnitude (90%) decline in population size over one generation. The Tuolumne River natural escapement declined by about 87% when the 2000-2002 generation declined from a total of 26,626 fish to a total 3,214 fish for the 2003-2005 generation. The likely cause of this decline is the extended drought conditions and low instream flow releases in the Tuolumne River from 2001 to 2004, which probably resulted in high juvenile mortality rates (see Smolt Outmigrant Production section below).

Hatchery Influence

Since 1996 when the increased Tuolumne River minimum instream flows began, the mean percentage of hatchery fish in the Tuolumne River escapement is estimated to be 21.3% (range 1.3% to 48.3%, Table 4). Although most of the hatchery fish in the Tuolumne River escapement were produced at the Merced River Hatchery, which is within the same diversity group as the Tuolumne River, and the Merced River Hatchery primarily provides small numbers of study fish and so generally follows "best management practices", the percentages of estimated hatchery fish in the Tuolumne River escapement exceed the Lindley et al. (2007) high risk criterion of less than 10% (3 generations) to 15% (1 to 2 generations) hatchery fish.

Potential Consequence of Reduced Genetic Diversity

A potential consequence of the Tuolumne River effective population declining to 157 salmon from 1990 to 1992 and the resulting loss of genetic viability is that the population's productivity declined by about 50% from 1996 to 2005 (Fig. 5) even though higher minimum instream flows were instituted, a barrier was installed at the head of the Old River in 1997 and 2000 to 2004 to improve smolt survival in the San Joaquin River Delta (SJRGA 2007), export rates at the Federal and State pumping facilities were reduced during the primary smolt migration period (SJRGA 2007), and habitat restoration, including spawning gravel augmentation, floodplain restoration, and predator pond isolation projects had been completed in the Tuolumne River (TID and MID 2005).

The methods used to estimate recruitment, which is the number of adult salmon that survived to Age 2, are described in Mesick et al. (2009b) using the natural escapement estimates in Table 4. The statistical tests of significance included Robust Inference and a Permutation Test conducted by Dr. Alan Hubbard[i]. He used these tests because they avoid the potential problem of autocorrelation in population trend analyses that would violate an assumption of correlation analyses. Dr. Hubbard's analysis indicates that the slopes of the regressions between the two data sets shown in Fig. 5 are marginally significantly different ($P = 0.01$ for the Robust Inference test and $P = 0.08$ for the Permutation Test). There were no significant differences in the intercepts for the two regressions. It is likely that the statistical significance of the difference between the slopes for the two time periods would increase ($P < 0.05$ for both tests), if the statistical

models could include the effects of spawner abundance and poor ocean conditions in 2005. However, there were too few estimates to include these variables in the tests.

Although there are no data to show that the population's productivity rate was directly affected by a loss of genetic viability, the likelihood that the Tuolumne River population was heavily repopulated with hatchery fish (Table 4) strongly suggests a causal link between genetic viability and population productivity. In 1993, of the total escapement of 471 salmon, 44% were naturally produced, 15% were San Joaquin River Basin Hatchery fish, and 41% were Sacramento River Basin hatchery fish (methods described in Mesick et al 2009a).
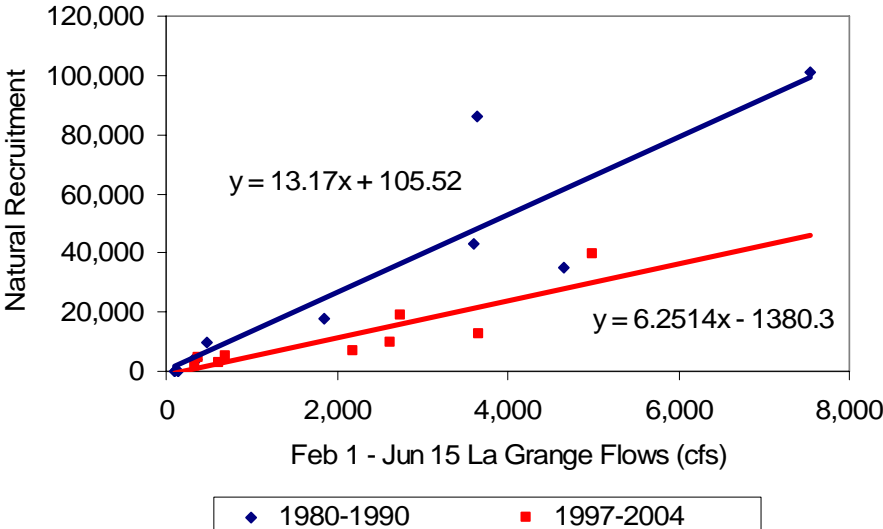
Fig. 5. Tuolumne River natural fall-run Chinook salmon recruitment plotted with mean flow in the Tuolumne River from the La Grange Dam (rkm 84) during February 1 through June 15 during two periods: 1980 to 1990 (pre-FSA) and from 1997 to 2004 (post-FSA). Recruitment is the number of adults in the escapement and ocean harvest (including shaker mortality) that belong to individual cohorts of same-aged fish (Mesick et al. 2009b). Estimates were excluded for which spawner abundance was less than 650 Age 3 equivalent fish to minimize the effect of spawner abundance on the relationship between flow and recruitment.

Environmental Factors That Affect Salmon Recruitment

I provide evidence that the production of Tuolumne River salmon is primarily determined by the instream flow releases from La Grange Dam as they affect juvenile survival in the Tuolumne River and provide attraction flows for migrating adult salmon to navigate back to the Tuolumne River. The salmon population is also affected by conditions that affect salmon survival in the San Joaquin Delta and the ocean, although these effects are relatively small or infrequent compared to the importance of instream flow releases. The following describes the factors that affect salmon escapement and/or recruitment relative

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to adult upstream migration, spawner abundance, spawning habitat and fry production, juvenile survival in the Tuolumne River, Delta, and ocean, and the harvest of adult salmon in the ocean.

Adult Upstream Migration

Up to 58% of the adult MRH fall-run Chinook salmon with CWTs that were recovered in Central Valley rivers during the fall-run Chinook salmon escapement surveys from 1979 to 2007 (Mesick et al. 2009a) strayed to the Sacramento River Basin when the 10-day mean flow in the San Joaquin River at Vernalis in late October was less than 3,500 cfs; whereas stray rates were less than 6% when flows were at least 3,500 cfs (Fig. 6). From 1996 to 2006, the mean stray rate was 14.6% (range 0% in 2006 to 43.5% in 1999). Adult salmon home to their natal streams in part by following olfactory cues from their natal stream (Quinn 2005) and presumably 1,200 cfs from each of the three San Joaquin River tributaries, including the Tuolumne River, is needed for at least a 10-day period in mid to late October for the salmon to home successfully. If these flows are provided, the stray rates should decrease from the existing mean of 14.6% to a mean of about 5%, and thereby increase Tuolumne River escapement by an average of 10%.
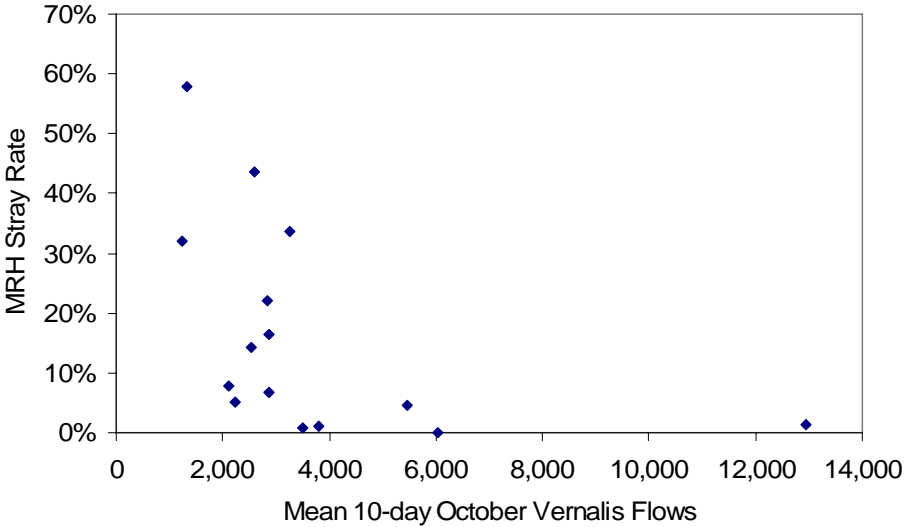
Fig. 6. The percentage of Merced River Hatchery fall-run Chinook salmon with CWTs (Mesick et al. 2009a) that were released in the San Joaquin River Basin upstream from Jersey Point as juveniles and then recovered as adults in the Sacramento River Basin relative to the adult recoveries in the Central Valley from 1983 to 1988 and from 1995 to 2003. Estimates for 1989 to 1994 were not used because there were fewer than a total of 1,000 CWTs in all Central Valley rivers during these years and so there was a high degree of uncertainty in the stray rate estimates. The mean Vernalis flows (USGS gauge 11303500) were computed for the 10-day period in mid to late October with the highest flows.

Spawner Abundance

Spawner abundance can affect juvenile salmon production in two ways. First, too few spawners results in low production of juveniles due to a lack of eggs. On the other hand, the limited availability of spawning habitat in the Tuolumne River could result in high rates of redd superimposition rates at high spawner abundances that could result in the mortality of the eggs of early spawners when late spawners dig up their redds. Most spawning in the Tuolumne River occurs in the upper 8 kilometers below La Grange Dam and extensive redd superimposition occurs in this area (TID and MID 2005).

My results suggest that adult recruitment is affected to only a slight degree by spawner abundance ranging between 434 and 39,347 Age 3 equivalent spawners based on a model that holds the effects of flow constant (Fig. 7). The relationship is primarily driven by the data associated with low flow (non flood control) releases that probably constrain the amount of habitat for juvenile salmon. Therefore, I conclude that during managed flow releases, the rearing habitat in the Tuolumne River can support the progeny of no more than about 434 adults and that redd superimposition has had no detectable effect on recruitment.
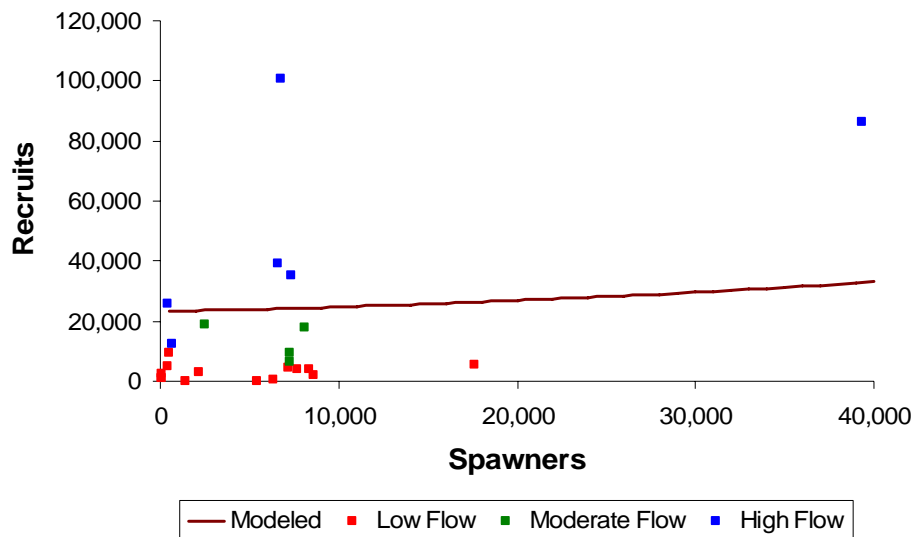
Fig. 7. The relationship between the number of natural recruits to the number of Age 3 equivalent spawners in the Tuolumne River from 1981 to 2004 segregated by low flows (<1,000 cfs) at La Grange Dam from 1 February to 15 June, moderate flows (1,000 to 2,999 cfs), and high flows (3,000 cfs to 7,540 cfs). The modeled relationship, which holds flow constant at 3,000 cfs, is based on multiple linear regression analysis between recruitment, the mean flow at La Grange Dam and quadratic terms for the number of Age 3 equivalent spawners including both hatchery and natural adults. The methods used to estimate natural recruitment and Age 3 spawner abundance are described in (Mesick et al. 2009b).

Spawning Habitat And Fry Production

Although the spawning habitat in the Tuolumne River has been extensively degraded, the production of fry is sufficient to saturate the rearing habitat in the lower Tuolumne River. The spawning habitat has been degraded by extensive in-river gold dredging and gravel mining during the first half of the 1900s, blocked gravel recruitment by the upstream dams, and 60,000 cfs flood control releases in January 1997 that washed away several key spawning beds and deposited tons of fine sediment in the remaining spawning beds (TID and MID 2005).

In spite of the degraded spawning habitat conditions, rotary screw trap studies conducted about 22 kilometers downstream from La Grange Dam in 1999 and 2000 indicated that the juvenile production was estimated to be at least 7,297,177 and 3,481,884 fish, respectively. Relative to the number of Age 3 equivalent spawners, the number of fry produced per spawner was 1,007 and 480 in 1999 and 2000, respectively, which indicates that 17% and 8% of the total number of eggs likely deposited in redds survived to a juvenile stage (fry, parr, and smolts) that began migrating into the lower river during 1999 and 2000, respectively. These estimates are relatively accurate for the period sampled because an adequate number (12-15) of trap efficiency tests were conducted that include tests with both fry and smolts at flows between 320 cfs and about 5,000 cfs (Vick et al. 2000, Hume et al. 2001). However, the actual number of juveniles produced would probably have been higher if sampling had begun in late December when fry begin migrating rather than on 19 January and 10 January for the 1999 and 2000 studies, respectively. It is likely that these numbers of juvenile produced far exceeded the capacity of the rearing habitat, because only 0.4% of these fish in 1999 and 1.4% of these fish in 2000 survived to a smolt-size at the downstream Tuolumne River trap at Grayson. The mean flows in 1999 and 2000 from 1 Mar to 15 June were slightly greater than 2,000 cfs, which is well above the minimum release requirements, and so juvenile survival rates would be expected to be even lower during minimum instream flow releases. These low juvenile survival rates provide strong evidence that the poor quality of the rearing habitat and the infrequent floodplain inundation is a substantial limiting factor for the Tuolumne River salmon population.

From 1999 to 2003, approximately 19,250 cubic yards of gravel was used to reconstruct spawning beds in the area near the La Grange Dam (TID and MID 2005). Although the reconstructed sites have not been highly used by Chinook salmon spawners compared to the pre-1997 conditions, it is unlikely that spawning conditions would have degraded further since 1997.

Juvenile Survival in the Tuolumne River

The survival of juvenile fall-run Chinook salmon that migrate from the Tuolumne River into the San Joaquin River and Delta is thought to be relatively low for fry and parr that must rear for a prolonged period before completing their migration to the ocean compared to the relatively high survival rates for smolt-sized juveniles. The mean

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recovery rates in the escapement for Coleman National Fish Hatchery (CNFH) fall-run Chinook salmon with CWTs that were released in the Sacramento River range between 0.29% to 0.45% for releases in January through April whereas the mean recovery rate is 1.98% for May releases, when the size of the CNFH juveniles is comparable to the size of the Tuolumne River smolts (methods described in Mesick et al. 2009a). The survival of fry and parr sized juveniles is low during dry and normal water years in the Central Delta, where the Tuolumne River smolts migrate, compared to the North Delta based on ocean recovery rates of CNFH fry with CWTs (Brandes and McLain 2001). The low survival rates of juveniles rearing in the Delta in dry and normal water years may be caused by a combination of factors such as predation, entrainment at numerous small, unscreened diversions, unsuitable water quality, high water temperatures, disease, and direct mortality at the state and federal pumping facilities in the Delta.

The number of smolt-sized outmigrants passing the Grayson rotary screw traps near the mouth of the Tuolumne River is highly correlated (adj-R^2 = 0.93, P = 0.001) with flow releases at the La Grange Dam from February 1 to June 15 from 1998 to 2005 (Fig. 8). This suggests that prolonged late winter and spring flows in the Tuolumne River are an important factor determining the survival rate of fry to the smolt-size of at least 70 mm fork length and that flows in excess of 3,000 cfs during fry rearing are important to their survival.
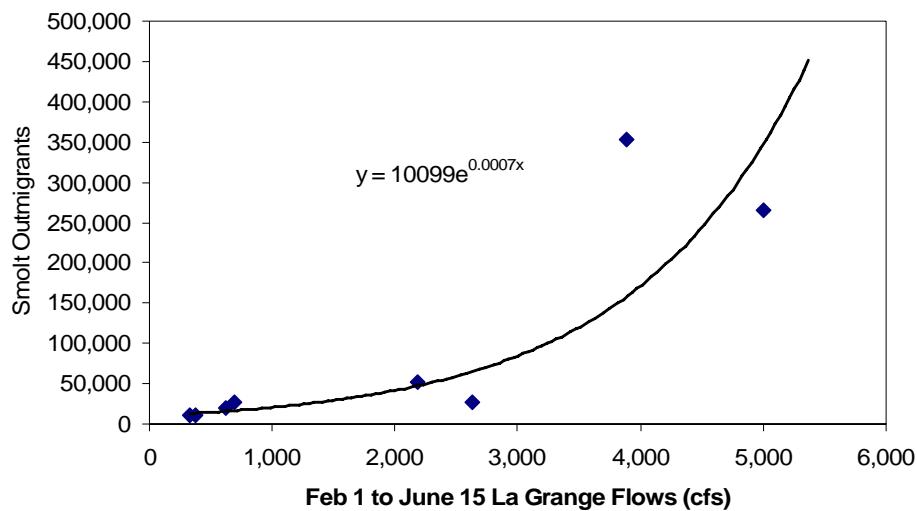
Fig. 8. The Number of smolt-sized Chinook salmon outmigrants (FL > 70 mm) passing the Grayson rotary screw trap site (rkm 8.4) plotted with flows at La Grange between March 1 and June 15 in the Tuolumne River from 1998 to 2005. The abundance of Age 3 equivalent spawners ranged from 1,645 in fall 2004 to 17,646 in fall 2000. The regression model has an R^2 of 0.93 and a probability level of 0.001. The spring 2006 estimates were omitted because the number of Age 3 equivalent spawners in fall 2005 was only 447 adults, which limited smolt production unlike the other years when flows were the primary determinant.

In most years, the number of smolt outmigrants from the Tuolumne River has been a good predictor of adult recruitment. The relationship between Tuolumne River adult

recruitment and spring flows from 1996 to 2005 (Fig. 9) is nearly identical to the relationship between smolt outmigrants and flows, except that there was a high mortality rate for the smolts in the ocean during spring 2005 that resulted in low adult recruitment.

It is likely that the survival of fry to a smolt-size in the Tuolumne River is dependent on prolonged flood control releases greater than 3,000 cfs because these releases result in the inundation of a substantial amount of floodplain habitat. Floodplain inundation between the La Grange Dam (rkm 84) and the Santa Fe Bridge (rkm 34) begins at a flow somewhere between 1,100 cfs and 3,100 cfs, when approximately 513 acres of overbank area become inundated (USFWS 2008). Floodplain inundation increases from 513 acres at 3,100 cfs to 823 acres at 5,300 cfs (USFWS 2008).

The relationship shows Natural Adult Recruits on the y-axis (0 to 45,000) versus Feb 1 to Jun 15 La Grange Flows (cfs) on the x-axis (0 to 6,000), with fitted quadratic curve:

$$y = 0.0019x^2 - 2.6014x + 6154.8$$

A data point labeled 2005 appears near 3,900 cfs at about 1,000 recruits.
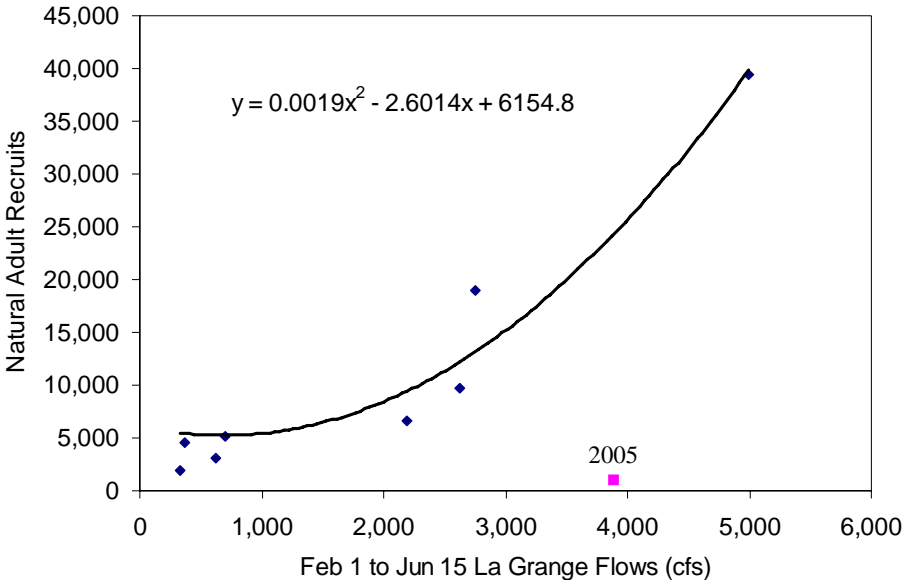
Fig. 9. The number of natural adult recruits relative to the average flow release from La Grange Dam from February 1 through June 15 when the cohorts migrated as juveniles toward the ocean from 1997 to 2005, when Age 3 equivalent spawner abundance was at least 1,007 fish. The quadratic equation computed by Excel is presented for the relationship for the estimates from 1997 to 2004.

Several recent studies document the importance of floodplain habitat to juvenile Chinook salmon in the Central Valley. Survival and growth rates of juvenile salmon were higher in inundated floodplain habitats in the Sacramento River's Yolo Bypass (Sommer et al. 2001) and Cosumnes River (Moyle 2000) than in the main channel. There is also extensive use of the seasonally inundated wetlands in the Sutter Bypass in lower Butte Creek by spring-run Chinook salmon fry that grow rapidly and outmigrate as smolts earlier than the juveniles that rear in the main creek channel (Ward and McReynolds 2001, Ward et al. 2002).

It is likely that the Tuolumne River floodplains improve juvenile survival when inundated by a combination of factors such as improved food availability, refuge from predators, and increased water temperatures in February and March that increase juvenile salmon growth rates. Floodplain inundation, particularly the ascending and descending limbs of the hydrograph, often provides most of the organic matter that drives aquatic food webs in rivers (Allan 1995) and aquatic productivity is related to area inundated in some rivers (Large and Petts 1996). Water temperatures were higher in the inundated floodplain habitats in the Yolo Bypass than in the main channel and the higher temperatures and the abundant food resources resulted in rapid growth rates (Sommer et al. 2001). It is also likely that inundated floodplains provide refuge for juvenile salmon from the abundant predatory fish in the Tuolumne River, which include largemouth bass (*Micropterus salmoides*), smallmouth bass (*M. dolomieu*), Sacramento pikeminnow (*Ptychocheilus grandis*), and striped bass (*Morone saxatilis*), although this has not been verified by studies.

Timing of Late Winter Floodplain Inundation – Since 1996, the management of instream flow releases from La Grange Dam has focused on pulse flows that began in mid to late April of at least 1,100 cfs for about 10 days to improve smolt survival. However, it is likely that late winter base flows usually less than 350 cfs during dry years resulted in high rates of juvenile mortality before the pulse flows were initiated, and therefore, there has been no substantial increase in the production of smolt outmigrants or adult recruitment since 1996.

Floodplain inundation must occur in February and/or March to improve the survival of fry to a smolt-size and to increase their growth rates so that they begin smoltification and their migration toward the ocean in early spring when water temperatures are most suitable for their survival. The smolting process is metabolically demanding and juveniles release hormones, including cortisol that inhibits their immune system, making smolts more vulnerable to disease and other stress (Quinn 2005). The upper water temperature threshold for the smoltification process that has been recommended by the EPA (2003) is 15°C.

When flood control releases averaged almost 5,000 cfs from 1 February to 15 June in the Tuolumne River in 1998, the smolts migrated from the river from mid March through at least mid June (Fig. 10). However, the required instream flow releases are inadequate to maintain water temperatures below the 15-degree threshold when smolts are migrating, except in mid March or when pulse flows of 1,200 to 1,400 cfs are made in mid to late April (Fig. 11). The mean daily water temperatures at Modesto (river kilometer 23.5) typically exceed the 15-degree threshold for smolts in early April and May during base flow releases (< 350 cfs) but usually decline to less than 15 degrees when pulse flows of at least 1,000 cfs are made in mid to late April (Fig. 11). However from mid May to mid June, flows may need to be increased to 5,000 cfs to maintain the 15-degree threshold near the mouth of the Tuolumne River based on the HEC5Q Water Temperature Model developed for the CalFed Ecosystem Restoration Program.
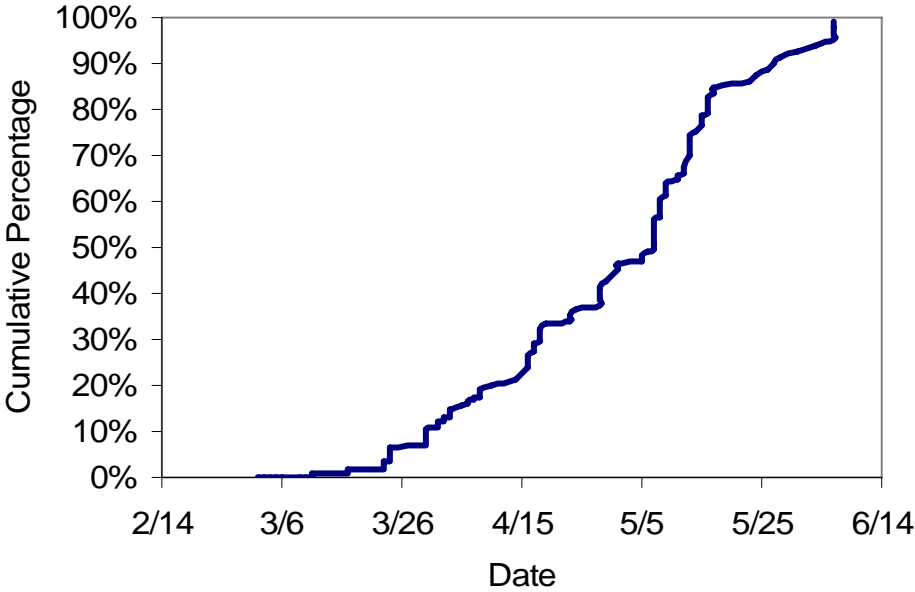
Fig. 10. Cumulative percentage of the number of smolt-sized (> 70 mm fork length) outmigrants passing the Grayson rotary screw trap in 1998, when trapping ceased on 6 June at a smolt passage rate of 2,800 (1.5%) per day.
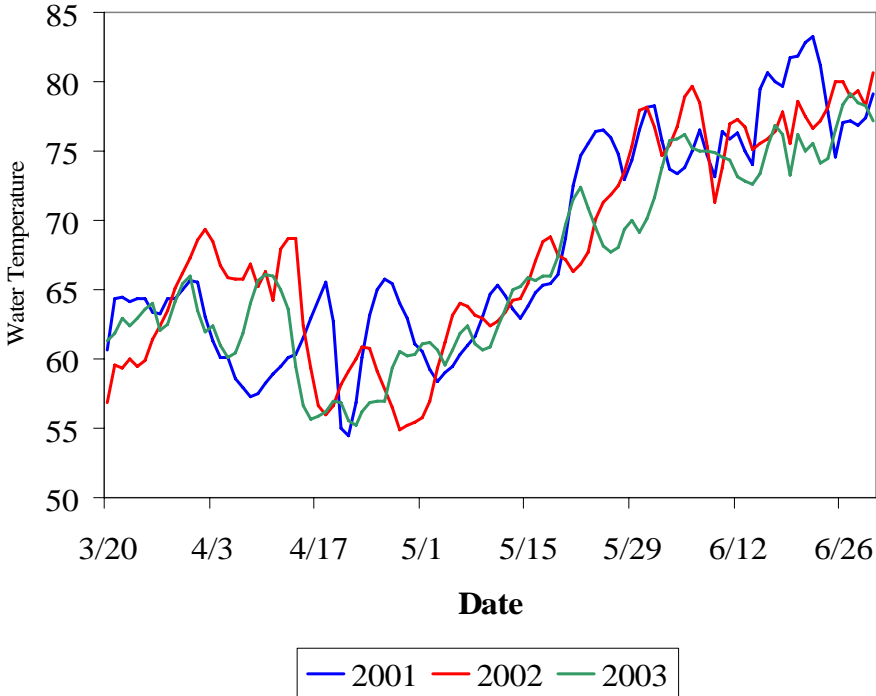
Fig. 11. The mean daily water temperature in the Tuolumne River near Modesto (river kilometer 23.5) during 2001 to 2003. Temperature estimates are provided by the California Department of Water Resources at the online Data Exchange Center. Pulse flows of at least 1,000 cfs were made from 24 April to 8 May 2001, 24 April to 1 May 2002, and 14 to 22 April 2003. The Modesto temperature gage did not function in spring 2004.

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Empirical evidence that pulse flows of at least 3,000 cfs that inundate the floodplain habitats during February and March increase fry survival is based on rotary screw trap studies conducted near the mouth of the Tuolumne River from 1999 to 2004. Even brief pulse flows doubled fry survival based on a comparison of the estimated abundance of smolt-sized juvenile salmon leaving the river in 2001 to 2004. During 2002 and 2003, when there were no late winter pulse flows (Fig. 12), the estimated number of smolt-sized juveniles that migrated from the Tuolumne River was 10,095 and 10,305, respectively. During 2001 and 2004, when there were 2- to 3-day winter pulse flows of about 3,000 cfs (Fig. 12), the estimated number of smolts migrating from the river increased to 26,370 in 2001 and 20,330 in 2004   During all four years, there were 8- to 10-day flows of 1,200 to 1,400 cfs in late April or early May (Fig. 12).
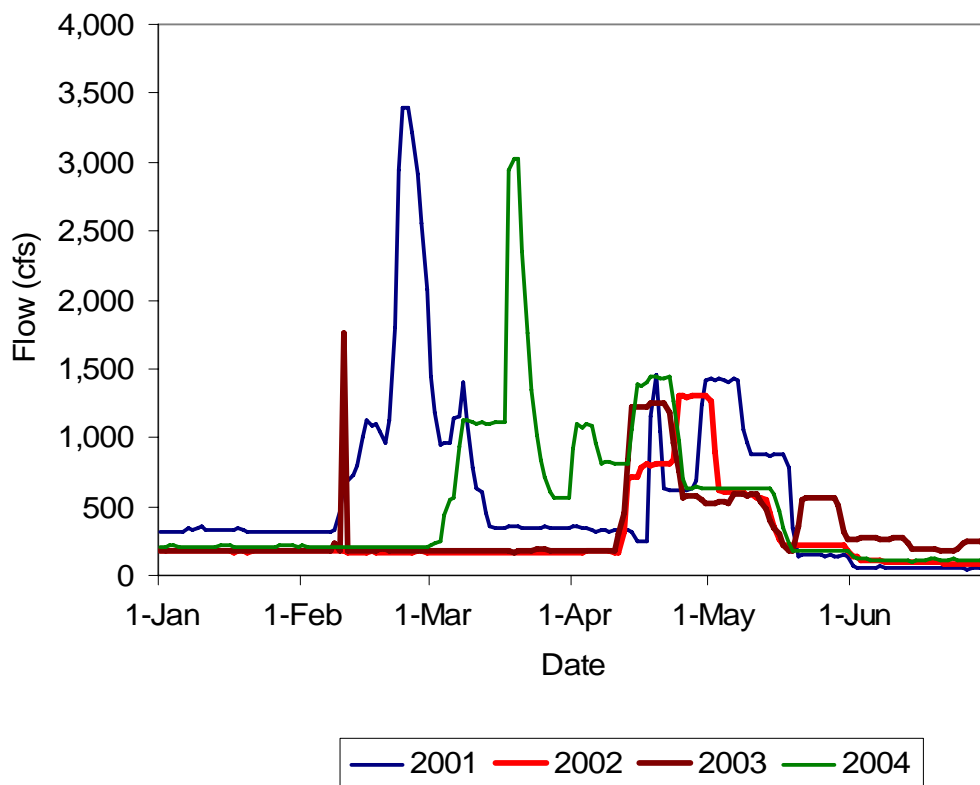
Fig. 12. Flows measured in the Tuolumne River at La Grange from 1 January to 30 June in 2001 to 2004. Two- to 3-day pulse flows occurred in late winter only in 2001 and 2004 whereas there were 8- to 10 day, 1,200 to 1,400 cfs pulse flows in mid to late April during all 4 years.

The other important benefit of the brief pulse flow releases is that the smolts migrated earlier in 2001 and 2004 when the pulse flows were made than in 2002 and 2003 when there were no pulse flows. The mean number of smolts passing the Grayson rotary screw traps in early April is 495 smolts per day (498 to 491) in 2001 and 2004, when the brief late winter pulse flows occurred, and 26 smolts per day (22 to 29) in 2002 and 2003, where there were no late winter pulses (Table 2). The cumulative percentage of smolts caught at the Grayson trap site by 15 April was also higher during 2001 when the late

winter pulses were made compared to 2002: 41.2% in 2001 and 8.4% in 2002; the rotary screw trap studies were started too late to provide accurate estimates for 2003 and 2004. This suggests that brief late winter pulse flows improve growth rates and thereby accelerate the smoltification process, which should lead to increased smolt survival rates through the lower Tuolumne River and Delta.

The evidence for the benefits of high late winter flows that inundate floodplain habitats is clearer for the Stanislaus River, where there are additional rotary screw trap estimates of the number of salmon juveniles produced in the spawning reach upstream of Oakdale (river kilometer 64.7) as well as rotary screw trap estimates of the number that survived to a smolt size and migrated from the river at Caswell state park (river kilometer 13.8) for a variety of flow releases. The Stanislaus River studies are appropriate to discuss here because the salmon are also strongly affected by late winter and spring pulse flows, the river is less than 16 kilometers to the north of the Tuolumne River, and both rivers have been extensively degraded by in-river gravel and gold mining and agricultural use of floodplain habitats. The estimates for spring 2000 indicate that when the flows at Ripon exceeded 3,000 cfs in late February and early March, 74% of the juvenile salmon that migrated past the upper trap survived their migration to the lower trap and that in April and most of May, there were substantially more juveniles leaving the river than passed the upper trap (Fig. 13). This suggests that many juveniles were able to grow to a smolt size in the lower river downstream from Oakdale in April and May even though the flows had declined to 1,000 cfs to 1,500 cfs.
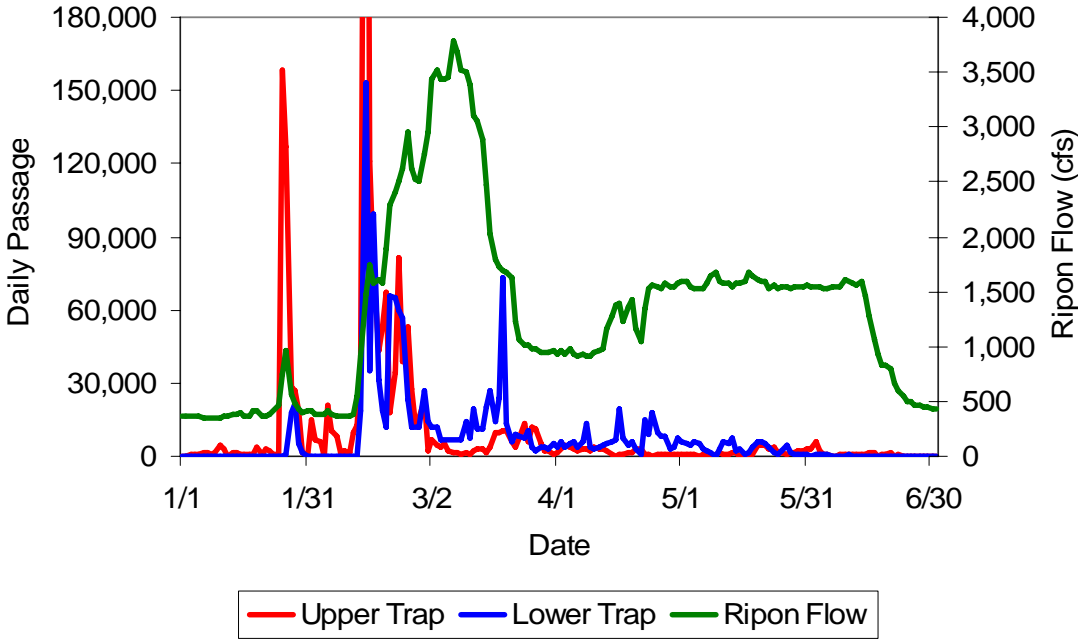
Fig. 13. Estimated daily passage of Chinook salmon fry and smolt-sized outmigrants at Oakdale (upper trap) and Caswell Park (lower trap) rotary screw traps plotted with mean daily flow at Ripon in Stanislaus River in 2000.

In contrast, juvenile survival in the Stanislaus River in spring 2001 was much lower when

there were no high flow releases in late winter (Fig. 14). In 2001, only 11% of the juveniles survived their migration between the upper and lower traps and there were fewer juveniles passing the lower trap in April and May compared to the number that passed the upper trap even during the 1,500 cfs pulse flow (Fig. 14). These results suggest that without late winter pulse flows, the smolts were in relatively poor health and few survived their downstream migration in spite of the 1,500 cfs pulse flows in late April and early May.
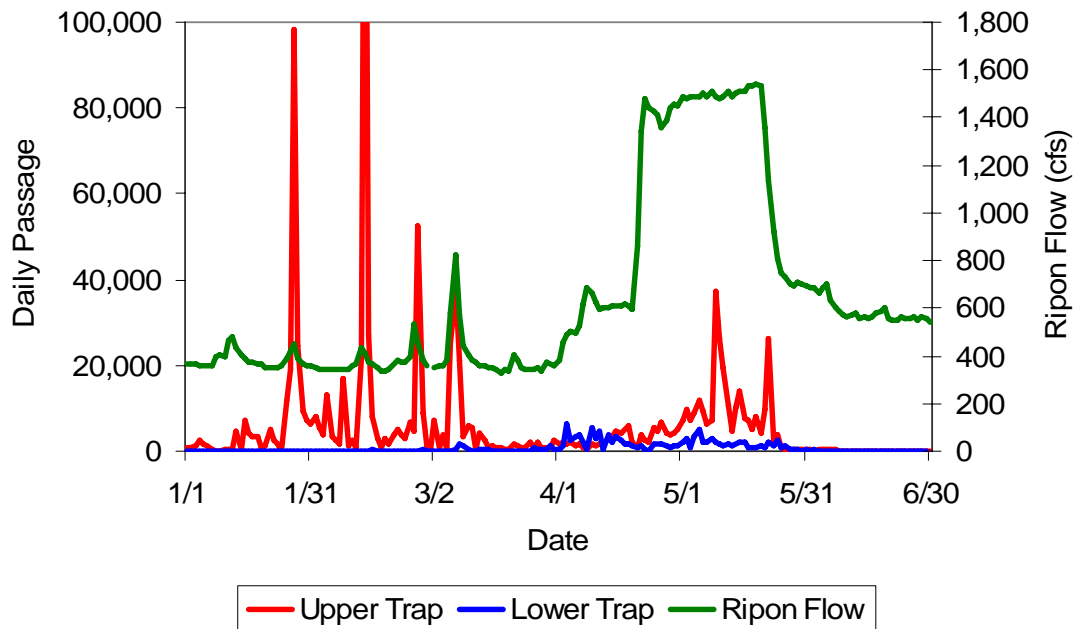
Fig. 14. Estimated daily passage of Chinook salmon fry and smolt-sized outmigrants at Oakdale (upper trap) and Caswell Park (lower trap) rotary screw traps plotted with mean daily flow at Ripon in Stanislaus River in 2001.

Importance of spring water temperatures - Although the rotary screw trap studies suggest that the brief late winter pulse flows in Tuolumne River in 2001 and 2004 approximately doubled the number of smolt-sized juvenile salmon that migrated from the river and caused a greater percentage of the smolts to migrate early in the season, there was only a 13% increase in adult recruitment in 2001 and 2004 compared to 2002 and 2003. The mean recruitment estimates for 2002 and 2003 is 4,129 adults (range 2,626 to 5,632) when there were no late winter pulse flows and 4,679 adults (range 3,274 to 6,084) for 2001 and 2004 when there were 2 to 5 day late winter pulse flows.

One possible explanation for the lower than expected increases in recruitment from the brief late winter pulse flows is that the water temperatures in the lower river exceeded the 15-degree threshold for smolts during early April and in May, when base flow releases were made (Fig. 11) and it is possible that high temperatures allowed disease(s) to progress and cause delayed mortality as the smolts migrated through the Delta. The USFWS conducted a survey of the health and physiological condition of juvenile fall-run Chinook salmon in the San Joaquin River and its primary tributaries, the Stanislaus,

Tuolumne, and Merced rivers, during spring 2000 and 2001 (Nichols and Foott 2002). *Renibacterium salmoninarum*, the causative agent of bacterial kidney disease (BKD), was detected in naturally produced juveniles caught in rotary screw traps from the Stanislaus and Tuolumne rivers and juveniles caught with a Kodiak trawl at Mossdale in the San Joaquin River. No gross clinical signs of BKD were seen in any of the fish examined. Other diseases, such as Proliferative Kidney Disease was detected in the Merced River (Nichols and Foott 2002) and Columnaris disease was detected in the Stanislaus River in 2007 by the USFWS, but not in the Tuolumne River, possibly due to the limited amount of testing conducted for disease. These diseases rapidly progress as water temperatures exceed a mean daily temperature of 15°C (Nichols and Foott 2002, Jones et al. 2007). Survival rates of Chinook salmon at 42 days postchallenge was 5% at 14°C in the laboratory (Jones et al. 2007) and so high mortality rates of outmigrating smolts could occur in the Delta or ocean.

The extent that the water temperatures exceeded the 15-degree threshold for smolts in early April is well correlated with the adult recruitment observed from 2001 to 2003, when water temperature data are available. Adult recruitment was the lowest at 2,626 adult recruits in spring 2002, when the pulse flows did not begin until 24 April. Prior to the pulse flow releases in 2002, the mean water temperatures at Modesto from 29 March to 14 April was 19.4 degrees, which substantially exceeded the 15 degree threshold (Fig. 11). In contrast, adult recruitment was higher, 6,084 and 5,632 adult recruits for spring 2001 and 2003, when the mean daily water temperatures were 16.1 degrees and 17.2 degrees in early April, respectively (Figure 11).

Recruitment and the abundance of smolt outmigrants were substantially higher in 1999 and 2000 when late winter flows exceeded 3,000 cfs from at least mid February to mid March and high flows releases kept water temperatures below or near the 15-degree threshold for smolts through mid May. In 1999, modeled water temperatures near the river's mouth were below the 15-degree threshold through 14 April and close to the threshold (mean 15.6°C, maximum 17.8°6) from 15 April 18 May (San Joaquin River Basin HEC5Q Water Temperature Model Developed for the CalFed Ecosystem Restoration Program). In 2000, modeled water temperatures near the river's mouth were below the 15-degree threshold through 1 April and close to the threshold (mean 16.1°C, maximum 18.3°C) from 2 April to 17 May (San Joaquin River Basin HEC5Q Water Temperature Model Developed for the CalFed Ecosystem Restoration Program cited in direct testimony of Gordus). The number of smolt-sized juveniles that migrated from the river in 1999 and 2000 was 26,832 and 52,132, respectively. This computes to an average increase of 387% compared to 2002 and 2003 when there were no late winter pulses. Adult recruitment was 9,293 and 12,103 in 1999 and 2000, respectively, which is 259% higher than the mean recruitment for 2002 and 2003, when there were no late winter pulses and water temperatures exceeded the 59-degree threshold in early April. It is likely that recruitment increased substantially by a mean of 259% in 1999 and 2000 primarily because the 59-degree threshold for smolts was not exceeded in late March and early April, compared to the 113% increase in 2001 and 2004 when the 59-degree threshold was exceeded. However, it is also likely that the high recruitment estimates for 1999 and 2000 would not have been possible without the late winter flows of at least 3,000 cfs that augmented the food supply, increased growth rates, and accelerated

smoltification and migration of the smolts so that a large percentage migrated by late April when water temperatures were below the 59-degree threshold.

Juvenile Survival In The Delta

CWT smolt survival studies have been conducted in the San Joaquin River to evaluate the effects of flow, Delta export rates, and the installation of a barrier at the head of the Old River which had the objective of minimizing the diversion of flow and juvenile salmon into the Old River, which led to the Federal and State pumping facilities in the Delta, from 1985 to 2004 (SJGRA 2007, Newman 2008). The results indicated that smolt survival was positively correlated with the flow in the San Joaquin River at Dos Reis and the installation of the Old River Barrier (Newman 2008). However, associations between the pumping rates at the State and Federal facilities and smolt survival were weak to negligible (Newman 2008). Therefore, flow releases in the Tuolumne River improve smolt survival in the Delta as well as in the Tuolumne River.

Juvenile Survival In The Ocean

The survival of Central Valley smolts entering the ocean during May and June (MacFarlane and Norton 2002) is probably the most critical phase for salmon in the ocean (Pearcy 1992, Mantua et al. 1997, Quinn 2005). Smolt survival in the ocean is highly correlated with food availability as affected by freshwater outflow from the estuary and coastal upwelling (Casillas 2007). The coastal areas provide abundant food resources for salmon smolts particularly when coastal upwelling provides cold, nutrient rich water and when high freshwater flows create a large interface area between freshwater and saltwater (Casillas 2007). Long-term records indicate that there are 15- to 25-year cycles of warm and cool periods that strongly correlate with marine ecosystem productivity (Mantua et al. 1997; Hollowed et al. 2001). However, more recent cycles have been relatively short with a cool productive cycle from July 1998 to July 2002, a warm unproductive cycle from August 2002 to July 2006, followed by cool productive cycle through at least July 2009 (Ocean Ecosystem Indicators 2008, web site provided by the Northwest Fisheries Science Center, NOAA Fisheries Service). Ocean productivity was particularly poor for the Gulf of the Farallones in 2005 and 2006 as indicated by the abandonment of nests on the Farallon Islands by Cassin's auklets, which have a similar diet compared to juvenile Chinook salmon, because of poor food availability (Sydeman et al. 2006; Wolf et al. 2009). The Pacific Decadal Oscillation is a basin-scale index of North Pacific sea surface temperatures and provides a good index of sea surface temperatures and has been correlated with Chinook salmon landings in California (Mantua et al. 1997).

An important local process that affects plankton production along the Oregon coast is coastal upwelling (Peterson et al. 2006). Upwelling is caused by northerly winds from April to September that transport offshore surface water southward and away from the coastline. This offshore, southward transport of surface waters is balanced by onshore northward transport of typically cool, high-salinity, nutrient-rich water that drives the marine food-web. The Coastal Upwelling Index (CUI) is based on the wind speed that drives coastal upwelling (Bakun 1973) and the CUI database is developed and distributed

by the Pacific Fisheries Environmental Laboratory, National Marine Fisheries Service's Southwest Fisheries Science Center, Pacific Grove, California. The survival of juvenile coho salmon (*O. kisutch*) is positively correlated with the April and mean April-May CUI values for Oregon coho salmon (Petersen et al. 2006) and the mean June to August curl-driven upwelling indices are positively correlated with growth rates of Chinook salmon in a tributary to the Smith River near the California-Oregon border (Wells et al. 2007). However, strong upwelling is not always correlated with high plankton productivity because the deep source waters for upwelling can be warm and nutrient poor (Peterson et al. 2006).

Tuolumne River fall-run Chinook salmon adult recruitment is poorly correlated with the mean CUI values from April through August for the Gulf of Farallones. For example, the relationship between mean CUI values for the May-June period, when most Central Valley smolts enter the ocean (MacFarlane and Norton 2002), with Tuolumne River recruitment (Fig. 15) shows the low recruitment for spring 2005 at low CUI values as expected, but also indicates that recruitment was high in 1986 and 1998 at similarly low CUI values. When incorporated into a multiple regression model with the mean La Grange flow from 1 February to 15 June and quadratic Age 3 equivalent spawner abundance variables, the CUI had negative coefficients for all periods from April through August, which is contrary to those reported for Oregon coho salmon (Peterson et al. 2006) and the Chinook salmon in the Smith River tributary (Wells et al. 2007). One explanation is that Tuolumne River fall-run Chinook salmon are primarily affected by instream flows in the Tuolumne River when the juveniles are rearing and migrating downstream, whereas ocean conditions would only have an effect during wet years, such as 2005 and 2006, when ocean conditions were unusually unproductive. On the other hand, the survival of hatchery raised salmon that are trucked to the Bay and Chinook salmon migrating in undamed rivers with frequent floodplain inundation such as the Smith River would be expected to be primarily affected by ocean conditions.

The mean May-June CUI is relatively high (240), indicating a high level of plankton productivity, during the 1996 to 2006 period compared to the 1981 to 1995 period (mean CUI = 213), and so changes in ocean productivity in the Gulf of Farallones do not explain the reduced recruitment productivity that occurred from 1996 to 2005 in the Tuolumne River.

Adult Harvest In The Ocean

Adult ocean harvest rates have declined since 1996 (Fig. 16) and so the decline in Tuolumne River escapement since 1996 cannot have been caused by the harvest of adult salmon in the ocean. My estimates of ocean harvest rates for all CWT Chinook salmon recovered during the fall-run Chinook salmon escapement surveys in the Central Valley from 1980 to 2007 (Mesick et al. 2009a, 2009b) indicate that the mean ocean harvest rate was 56% from 1980 to 1995 and 42% from 1996 to 2007. The Central Valley Index of Ocean Harvest (CVI), which is estimated each year by the Pacific Fishery Management Council (PFMC 2008) by dividing total harvest south of Point Arena by the total hatchery

and natural escapement to all Central Valley rivers, averaged 69% from 1980 to 1995 and 46% from 1996 to 2007.
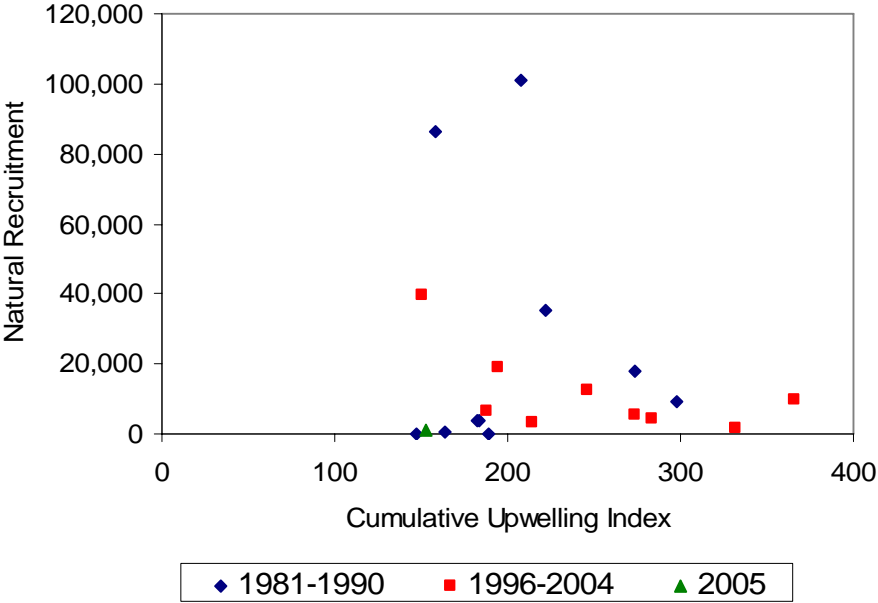

Fig. 15. The relationship between Tuolumne River naturally produced adult fall-run Chinook salmon recruitment and the mean Cumulative Upwelling Index at 37.5°N latitude (Gulf of the Farallones) for May and June from 1981 to 2005.
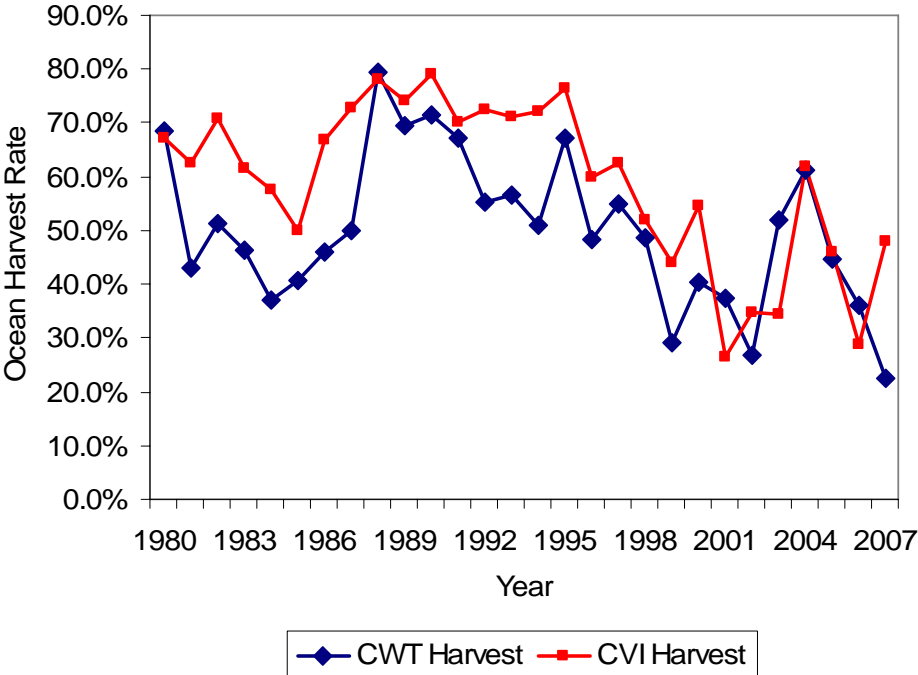
Fig. 16. Estimated rates of ocean harvest of Central Valley fall-run Chinook salmon from 1980 to 2007 in the combined commercial and sport fisheries based on CWT

recovery estimates (Mesick et al. 2009a, 2009b) and the Central Valley Index (PFMC 2008).

DISCUSSION

The above analyses indicate that the Tuolumne River fall-run Chinook salmon population is at a high risk of extinction since 1996 due to inadequate instream flow releases from La Grange Dam, primarily when juvenile salmon are rearing and outmigrating in late winter and spring and to a lesser extent during late October when adult salmon are migrating upstream. It is likely that the low escapements observed since 2005 have resulted in a decline in the population's genetic diversity, which puts the population at risk of extinction (Allendorf 1997, Lindley et al. 2007). The results also suggest that the extreme decline in escapement during the 1987 to 1992 drought and resulting decline in genetic diversity caused a 50% reduction in the population's productivity.

To maintain the Tuolumne River fall-run Chinook salmon population at a low risk of extinction, it will be necessary to increase the population in regard to all four of the Lindley et al. (2007) risk of extinction criteria. First, it will be necessary to increase the dry water year flow releases to keep escapement above 833 fish. Second, it will be necessary to increase normal water year flow releases to double the escapements and thereby reduce the rate of decline between wet-year escapements and dry-year escapements from 19.2% annually to 10% or less annually and reduce the percentage of hatchery fish in the escapement from 21.3% to about 10%.

To keep escapement above 833 fish during Critical and Dry water year types, when the San Joaquin Water Year Index is 2.5 MAF or less, it will be necessary to implement a flow schedule that includes: (1) a 10-day, 1,200 cfs late October pulse flow release to minimize adult straying; (2) a 2-day, 3,000 cfs pulse flow release in late February to increase fry survival and to accelerate both the smoltification process and smolt migration timing; and (3) flow management for La Grange Dam releases to keep water temperatures throughout the river below a threshold of 59°F from 20 March through at least 20 April to improve smolt survival. Releasing the 1,200 cfs fall pulse flows each year to minimize the percentage that stray to the Sacramento River Basin to no more than 6% would be expected to increase the mean recruitment for the 1996 to 2005 period from the observed 10,254 recruits under existing conditions to 12,054 adult recruits with the improved fall pulse flows, which computes to a possible 17.5% increase in recruitment (i.e., escapement). However, reducing stray rates alone would still not elevate the Tuolumne River population to a low risk of extinction, because escapement would still have declined to 1,241 adults from 2006 to 2008, the population would decline at an average annual rate of 19.9% from 1999 to 2008, and the percentage of hatchery fish would be 17.3%. There is uncertainty regarding the effectiveness of a brief late winter pulse flow and managing spring water temperatures to a threshold of 15°C primarily because they have not be used in concert before. However theoretically, implementing all three pulse flows should be effective at keeping escapement above 833 adult salmon

when ocean food resources for juvenile salmon are not exceptionally poor, as they were in 2005 and 2006.

To minimize the magnitude in population fluctuations and reduce the percentage of hatchery fish in the population to less than 10%, it will be necessary to implement flow schedules that extend the duration for late winter pulse flows to 14 days in Below Normal and Above Normal water year types and to 21 days in Wet water year types.   The recommended 59-degree Fahrenheit threshold should be maintained from 20 March to 30 April in Below Normal water year types and to at least 15 May in Above Normal and Wet water year types.

Another recommendation is to gradually ramp down the flood control releases during early summer to improve the recruitment of riparian tree species and thereby augment the amount of organic matter, shade, and woody debris and thereby improve the habitat quality for juvenile salmon. Research on a variety of cottonwood and willow species suggests that 1 to 1.5 inches/day is the maximum rate of water table decline for seedling survival (McBride et al. 1989; Segelquist et al. 1993; Mahoney and Rood 1993, 1998; Amlin and Rood 2002). Ramping down is necessary so that the root growth of the tree seedlings can keep up with the decline in the groundwater table as flows recede. Ramping rates of 100 to 300 cfs/day in the San Joaquin Basin are thought to prevent seedling desiccation under the assumed 1 inch/day maximum root growth rate.

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Table 1. The mean percentage of Chinook salmon with CWTs recovered in the Tuolumne River relative to the number released in the Bay-Delta, mainstem Sacramento and San Joaquin rivers, and tributaries from the Feather River Hatchery, Mokelumne River Fish Facility, Merced River Hatchery, and the Nimbus Fish Hatchery by month of release and age of adult salmon recovered in the escapement from 1981 to 2007 and for the 1987 to 1992 drought years (Age-D). The number of CWT lots (CWTs), years with CWT releases (Years), number of tagged and associated untagged juveniles released (# CWTs), and the number of unassociated untagged juvenile salmon released are also presented by month.

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Bay-Delta Releases												
Feather River Hatchery												
Age 2		0.00000%	0.00110%	0.00147%	0.00060%	0.00000%	0.00000%	0.00000%	0.00000%	0.00000%	0.00557%	
Age 3		0.00000%	0.00023%	0.00127%	0.00053%	0.00331%	0.00000%	0.00000%	0.00000%	0.00000%	0.02686%	
Age 4		0.00000%	0.00000%	0.00035%	0.00005%	0.00000%	0.00000%	0.00917%	0.00000%	0.00000%	0.00000%	
Age 2-D				0.00000%	0.00000%	0.00000%						
Age 3-D				0.00000%	0.00000%	0.00000%						
Age 4-D				0.00000%	0.00000%	0.00000%						
CWTs	0	23	43	95	201	202	81	49	2	4	13	0
Years	0	5	6	14	18	16	6	6	1	2	4	
# CWTs	0	606,636	1,520,758	13,728,108	23,315,464	14,413,217	4,650,592	2,200,750	85,408	215,875	638,056	0
Non-CWTs			292,000	11,786,382	39,620,644	46,308,815	27,195,991	17,048,815	5,095,540	433,160		
Mokelumne River Fish Installation												
Age 2				0.00074%	0.00011%	0.00000%	0.00000%		0.00000%	0.00000%	0.00000%	
Age 3				0.00209%	0.00353%	0.00321%	0.00000%		0.00470%	0.00782%	0.00000%	
Age 4				0.00025%	0.00131%	0.00000%	0.00000%		0.00000%	0.00000%	0.00000%	
Age 2-D				0.00000%	0.00000%	0.00000%						
Age 3-D				0.00000%	0.00000%	0.00000%						
Age 4-D				0.00000%	0.00000%	0.00000%						
CWTs				168	136	47	15		18	33	6	
Years				9	10	7	2		2	2	2	
# CWTs				12,197,656	32,857,855	25,409,233	534,777		2,066,760	1,027,431	208,020	
Non-CWTs	1,930,530	2,209,412	721,574	14,458,819	22,961,208	17,280,915	7,274,488	2,896,049	1,113,617	1,784,065	407,208	30,030

Merced River Hatchery

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Age 2				0.03498%	0.02393%					0.00000%		
Age 3				0.07362%	0.04933%					0.05690%		
Age 4				0.00672%	0.00670%					0.00000%		
Age 2-D				0.01155%	0.00530%	BY 1988						
Age 3-D				0.02059%	0.00629%	BY 1988						
Age 4-D				0.00000%	0.00000%	BY 1988						
CWTs				41	39					9		
Years				6	7					3		
# CWTs				1,057,024	1,250,090					277,245		
Non-CWTs			100			867,700						

Nimbus Fish Hatchery

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Age 2		0.00000%	0.00000%		0.00081%	0.00046%	0.00000%	0.00000%				
Age 3		0.00000%	0.00000%		0.00071%	0.00014%	0.00000%	0.00000%				
Age 4		0.00000%	0.00000%		0.00068%	0.00016%	0.00054%	0.00000%				
CWTs		1	1		24	44	32	4				
Years		1	1		1	4	4	1				
# CWTs		50,970	49,395		16,503,100	13,010,547	1,785,576	200,066				
Non-CWTs	815,200			3,499,247	18,026,535	53,465,226	20,307,755	2,424,105	270,281			

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Mainstem River Releases												
Feather River Hatchery												
Age 2		0.00000%	0.00000%	0.00000%	0.00018%	0.00000%	0.00000%	0.00000%				
Age 3		0.00000%	0.00000%	0.00072%	0.00005%	0.00000%	0.00000%	0.00000%				
Age 4		0.00000%	0.00000%	0.00000%	0.00029%	0.00000%	0.00000%	0.00000%				
CWTs		166	67	292	237	69	3	2				
Years		7	8	17	20	4	1	1				
# CWTs		3,867,364	2,156,924	11,848,267	11,897,739	3,518,521	83,025	72,008				
Non-CWTs	613,920		8,394	257,944	2,133,427	2,845,341	983,650	36,000			157,500	42,100
Mokelumne River Fish Installation												
Age 2				0.00469%	0.00000%					0.00000%	0.00000%	
Age 3				0.00000%	0.00000%					0.00000%	0.02708%	
Age 4				0.00000%	0.00000%					0.00000%	0.00000%	
CWTs	1			13	7					5	12	
Years	1			1	1					1	2	
# CWTs	14,290			335,314	180,666					214,043	469,078	
Non-CWTs	126,700			472,840	0	514,350				1,843,993	1,412,737	328,700
Merced River Hatchery												
Age 2				0.05664%	0.01039%					0.03841%	0.00000%	
Age 3				0.08079%	0.02469%					0.07954%	0.00000%	
Age 4				0.03080%	0.00399%					0.00000%	0.00000%	
CWTs				181	84					32	7	
Years				11	7					4	1	
# CWTs				5,207,336	3,446,630					935,259	326,430	
Non-CWTs				157,945	233,664	80,218						
Nimbus Fish Hatchery												
CWTs/Years	1		1									
# CWTs	48000		48,720									
Non-CWTs	8,349,320	11,639,846	12,528,241	8,370,510	6,220,315	12,387,395			150,960	223,880	121,660	

Tributary Releases

Feather River Hatchery

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Age 2	0.00000%	0.00000%	0.00000%	0.00000%	0.00000%	0.00000%				0.00000%	0.00000%	
Age 3	0.00000%	0.00000%	0.00000%	0.00000%	0.00000%	0.00215%				0.01679%	0.00000%	
Age 4	0.00000%	0.00000%	0.00000%	0.00000%	0.00000%	0.00000%				0.00000%	0.00000%	
CWTs	4	30	42	72	69	34				8	12	
Years	3	3	7	8	8	4				3	3	
# CWTs	792,330	1,099,592	2,773,111	3,738,407	4,146,314	3,566,645				5,479,069	2,723,738	
Non-CWTs	13,822,471	8,228,948	8,999,798	2,462,040	161,640	359,810	62,836		119,884	8,816,921	932,735	2,943,787

Mokelumne River Fish Installation

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Age 2				0.00000%	0.00000%	0.00000%			0.00000%	0.00000%	0.00000%	
Age 3				0.00527%	0.00000%	0.00000%			0.00000%	0.00000%	0.00000%	
Age 4				0.00000%	0.00000%	0.00000%			0.00000%	0.00000%	0.00000%	
CWTs				43	41	6			10	48	3	
Years				3	5	2			2	6	1	
# CWTs				668,364	1,195,358	177,882			3,858,022	5,404,300	144,900	
Non-CWTs	34,437	2,221,822	337,238	1,461,476	4,610,822	710,070	71,792	27,000	399,950	1,119,411	303,234	27600

Merced River Hatchery

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Age 2		0.02204%	0.00000%	0.00137%	0.00569%					0.00305%	0.00177%	
Age 3		0.20898%	0.00000%	0.00549%	0.02717%					0.00000%	0.00582%	
Age 4		0.01582%	0.01369%	0.00130%	0.00444%					0.00000%	0.00105%	
CWTs		3	7	236	121					15	25	
Years		1	2	13	9					4	3	
# CWTs		50,388	196,214	6,587,958	3,264,254					1,082,249	729,108	
Non-CWTs	4150	9,957	300,427	462,685	2,717,349	316,618				195,000	818,956	

Nimbus Fish Hatchery

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
# CWTs	0	0	0	0	0	0	0	0	0	0	0	0
Non-CWTs	16,562,691	21,157,730	4,302,638	2,889,732		544,625						7,193,652

Table 2. The dates when rotary screw trapping started and stopped at the Shiloh site in 1998 and at the Grayson site from 1999 to 2006, the mean expanded abundance estimate of juvenile salmon passing the traps per day (Fish/Day) during the beginning and/or final period of sampling, and the number of days during the beginning and/or final period of sampling used to compute the mean estimates of the number of fish passing the trap per day.

| | | Sampling Start Period | | | | Sampling End Period | | |
Year	Date Sampling Began	Mean Fish/Day 3/20 to 3/29	Mean Fish/Day 4/2 to 4/10	Number of Unsampled Days	Date Sampling Ended	Mean Fish/Day	Number of Unsampled Days	Percentage Adjustment in Abundance Estimate
1998	15-Feb	1,695	2,039	--	6-Jun	5,600	2	23.5%
1999	12-Jan	91	127	--	6-Jun	24	4	0.8%
2000	9-Jan	107	70	--	27-May	44	5	1.6%
2001	3-Jan	93	498	--	22-May	61	4	5.9%
2002	15-Jan	42	22	--	31-May	36	6	5.6%
2003	1-Apr	--	29	12	19-May	63	4	24.8%
2004	1-Apr	--	491	15	26-May	102	8	56.9%
2005	2-Apr	--	389	14	17-Jun	324	8	1.5%
2006	25-Jan	398	1,781	--	21-Jun	397	8	0.0%

Table 3. Estimates of the observed natural escapements (Exhibit 2), stray rates of CWT
Merced River Hatchery fish (Exhibit 2), improved stray rates if adequate pulse
flows had been released each year to keep stray rates at or below 6%, the
estimated changes in stray rates, and the estimates of "no-stray" escapements and
natural recruitment from 1980 to 2008.

Year	Observed Escapement	Observed Stray Rate	Improved Stray Rate	Stray Rate Change	Escapement Increase	No Stray Escapement	Stray Adjusted Natural Escapement	Stray Adjusted Natural Recruitment
1980	--	--	--	--	--	--	--	45,079
1981	14,253	0.7%	0.7%	0.0%	0	14,253	14,160	9,889
1982	7,126	17.4%	6.0%	11.4%	812	7,938	6,696	35,697
1983	14,836	9.2%	6.0%	3.2%	475	15,311	13,943	100,906
1984	13,689	0.8%	0.8%	0.0%	0	13,689	13,579	17,890
1985	40,322	0.9%	0.9%	0.0%	0	40,322	39,946	4,074
1986	7,404	3.4%	3.4%	0.0%	0	7,404	7,149	89,192
1987	14,751	12.3%	6.0%	6.3%	929	15,680	13,869	4,241
1988	5,779	6.6%	6.0%	0.6%	35	5,814	5,430	817
1989	1,275	21.3%	6.0%	15.3%	195	1,470	1,198	350
1990	96	95.5%	6.0%	89.5%	86	182	90	341
1991	77	38.4%	6.0%	32.4%	25	102	72	1,485
1992	132	19.9%	6.0%	13.9%	18	150	124	1,365
1993	471	56.4%	6.0%	50.4%	237	708	443	3,647
1994	506	25.4%	6.0%	19.4%	98	604	476	6,024
1995	827	21.4%	6.0%	15.4%	127	954	778	35,547
1996	4,362	31.5%	6.0%	25.5%	1,112	5,474	4,101	11,984
1997	7,146	28.7%	6.0%	22.7%	1,622	8,768	6,719	27,898
1998	8,910	18.1%	6.0%	12.1%	1,078	9,988	8,375	35,790
1999	8,232	16.2%	6.0%	10.2%	840	9,072	7,736	9,868
2000	17,873	10.9%	6.0%	4.9%	876	18,749	16,800	14,233
2001	8,782	20.3%	6.0%	14.3%	1,256	10,038	8,251	7,149
2002	7,173	48.3%	6.0%	42.3%	3,034	10,207	6,742	3,004
2003	2,163	35.8%	6.0%	29.8%	645	2,808	2,033	6,315
2004	1,984	38.7%	6.0%	32.7%	649	2,633	1,864	3,313
2005	719	15.0%	6.0%	9.0%	65	784	676	987
2006	625	7.6%	6.0%	1.6%	10	635	587	--
2007	224	1.3%	1.3%	0.0%	0	224	221	--
2008	455	4.6%	4.6%	0.0%	0	455	434	--

Table 4. The Department of Fish and Game estimated escapement of fall-run Chinook Salmon in the Tuolumne River (GrandTab), the estimated total number of marked (coded-wire tag and adipose clipped) hatchery adults that returned to the Tuolumne River, the estimated number of unmarked hatchery adults from the Mokelumne, Nimbus, Feather, and Merced river hatcheries that returned to the Tuolumne River, the escapement of naturally produced and hatchery produced adults, and the percent hatchery fish in the escapement from 1981 to 2008. The 2008 marked hatchery adult estimates are presented in Ford and Kirihara (2009), which do not include the unmarked assocated releases of juvenile fish, which are included for all other estimates.

| | Total Escapement | Marked Hatchery Adults | Unmarked Hatchery Adults | | | | Estimated Natural Escapement | Estimated Hatchery Escapement | Percent Hatchery |
			Mokelumne Hatchery	Nimbus Hatchery	Feather River Hatchery	Merced River Hatchery			
1981	14,253	50	31	9	3	0	14,160	93	0.7%
1982	7,126	753	439	41	10	0	5,883	1,243	17.4%
1983	14,836	339	5	515	508	0	13,468	1,368	9.2%
1984	13,689	31	1	33	46	0	13,579	110	0.8%
1985	40,322	272	31	46	28	0	39,946	376	0.9%
1986	7,404	156	6	22	71	0	7,149	255	3.4%
1987	14,751	1,672	87	3	28	21	12,940	1,811	12.3%
1988	5,779	279	6	0	0	99	5,395	384	6.6%
1989	1,275	179	9	37	4	43	1,003	272	21.3%
1990	96	70	8	12	0	2	4	92	95.5%
1991	77	20	6	0	0	3	47	30	38.4%
1992	132	23	0	3	0	0	106	26	19.9%
1993	471	114	0	46	105	0	205	266	56.4%
1994	506	106	2	18	0	2	378	128	25.4%
1995	827	142	5	10	15	5	650	177	21.4%
1996	4,362	1,057	54	5	87	170	2,988	1,374	31.5%
1997	7,146	1,328	11	1	0	709	5,097	2,049	28.7%

	Total Escapement	Marked Hatchery Adults	Unmarked Hatchery Adults				Estimated Natural Escapement	Estimated Hatchery Escapement	Percent Hatchery
			Mokelumne Hatchery	Nimbus Hatchery	Feather River Hatchery	Merced River Hatchery			
1998	8,910	1,422	56	69	21	45	7,297	1,613	18.1%
1999	8,232	1,061	32	86	77	80	6,896	1,336	16.2%
2000	17,873	1,321	256	6	0	366	15,924	1,949	10.9%
2001	8,782	1,591	54	4	0	138	6,995	1,787	20.3%
2002	7,173	2,742	553	0	64	106	3,707	3,466	48.3%
2003	2,163	565	127	0	38	45	1,388	775	35.8%
2004	1,984	472	229	0	32	35	1,215	769	38.7%
2005	719	87	0	0	0	21	611	108	15.0%
2006	625	8	0	0	0	40	577	48	7.6%
2007	224	0	0	0	0	3	221	3	1.3%
2008	455	≥ 21	?	?	?	?	≤ 434	≥ 21	$\geq 4.6\%$

List of End Notes

[i] Dr. Alan Hubbard, Assistant Professor of Biostatistics (Division of Biostatistics, School of Public Health, University of California, 101 Haviland Hall, MC 7358, Berkeley, CA 94720